EFFECTS OF HARVEST ON WOLF SOCIAL STRUCTURE, POPULATION DYNAMICS, AND VIEWING OPPORTUNITIES IN NATIONAL PARKS

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A

DISSERTATION

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

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Fairbanks, Alaska

August 2015

Abstract

Management of gray wolves (*Canis lupus*) in and adjacent to Denali National Park and Preserve (DNPP) is complex. Wolves that live primarily within the park, where they are protected from harvest, often range across the boundary of the park where harvest of wolves is legal. Protection of wolves within the park provides for wolf viewing opportunities along the Denali Park Road for tens of thousands of visitors annually. Additionally, there is interest in maintaining wolf harvest opportunities adjacent to the park. The objectives for wolf viewing and harvest have been perceived as in direct conflict, but quantitative analysis of the relationship was lacking.

Harvest of wolves is a highly contentious conservation and management issue worldwide, with unknown population-level consequences. The impact of the loss of reproductive individuals (breeders) may be particularly important to wolf pack structure, reproduction and population dynamics. I evaluated the effect of breeder loss on social stability, recruitment and population growth of wolves in DNPP and found that breeder loss preceded 77% of cases (n = 53) of pack dissolution from 1986 to 2012. Packs were more likely to dissolve if a female or both breeders were lost and pack size was small. Harvest of breeders increased the probability of pack dissolution, likely because the timing of harvest coincided with the breeding season of wolves. Breeder mortality and pack dissolution had no significant effects on immediate or longer-term population dynamics.

I examined the effect of legal harvest of wolves along the boundaries of DNPP and Yellowstone (YNP), on wolf viewing opportunities within the parks during peak tourist season. Although sightings were largely driven by wolf population size and proximity of den sites to roads,

sightings in both parks were significantly reduced by harvest. Sightings in YNP decreased by 31% following years with harvest of a wolf from a pack and sightings in DNPP decreased by 57% during the absence of a harvest buffer zone relative to years with the buffer.

Controlling for variables influencing both the probability of wolf presence near the road and the detection of wolves, we found that the presence of a wolf harvest buffer zone adjacent to the park increased wolf sightings along the Denali Park Road. The effect of the harvest buffer on sightings was similar in magnitude to an increase in pack size by two wolves or more than a two-fold decrease in masking vegetation.

These results suggest that harvest adjacent to park has the potential to substantially reduce wolf sightings. Harvest of wolves adjacent to protected areas can reduce sightings within those areas despite minimal impacts on the size of protected wolf populations. Consumptive use of carnivores adjacent to protected areas may therefore reduce their potential for non-consumptive use, and these tradeoffs should be considered when developing regional wildlife management policies.

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Acknowledgements

I would like to thank several funding sources for their support. The National Park Service provided major funding for the project and my salary. The Department of Biology and Wildlife, Institute of Arctic Biology, and the Graduate School at the University of Alaska Fairbanks provided travel grants for me to attend conferences and visit Yellowstone National Park which helped establish a valuable and on-going collaboration. Additional funding was provided by National Science Foundation grant DEB-1245373, the Yellowstone Park Foundation, and an anonymous donor for the work in Yellowstone National Park. The Alaska Department of Fish and Game and United States Geological Survey provided valuable assistance, data, and in-kind support for staff time. This research would not have been possible without the help of volunteers Nick Bromen, Jessica Drain and Robin Rausch, who meticulously read through pages and pages of field notes. Carol Piser helped me to navigate administrative obstacles during my time as a graduate student. Christine Hunter provided helpful guidance and discussions during the early phase of the project. I was extremely fortunate to have Laura Prugh as my advisor. She challenged and supported me and was always available to talk and think through questions and problems as they arose. My committee members Scott Brainerd, Jeff Falke, Grant Hilderbrand and Mark Lindberg all provided valuable insight, guidance and mentorship and greatly improved the quality of this dissertation.

I would like to thank the members of the Prugh lab, who helped broaden my perspective in the field of science and in life. My friends (the entire Stampede crew) provided much needed diversions and laughter. I especially want to thank my mom who never failed to support me, my husband Jared, who shouldered the load of the work for our daily life for several years without complaint and was unfailing in his love and encouragement, and my daughter, Juniper, who gave me a reason to smile and laugh every day. Most of all I want to thank my dad for being my inspiration to persevere and seek a graduate education.

This work would never have been accomplished if it weren't for Dave Mech, Layne Adams, John Burch, Bruce Dale and Tom Meier who pioneered the long term study wolf study in Denali National Park and Preserve and collected data from 1986 to 2012. I want to dedicate this dissertation to my mentor, Tom Meier, who asked me why the hell I wanted to get a PhD but supported me in pursuing it nonetheless.

Chapter 1

General Introduction

1.1 Application of Structured Decision Making to a complex management issue

Movement of terrestrial wildlife across jurisdictional boundaries is a common and persistent issue in wildlife management. The issue of transboundary management is particularly relevant for large carnivores. The majority of the world's large carnivores are currently threatened (Ripple et al. 2014) and, while refuges play a vital role in preserving these populations around the globe (Brashares et al. 2001), these wide ranging species are sensitive to human impacts outside and even inside of these protected areas (Woodroffe & Ginsberg 1998). In North America, transboundary management issues occur in several areas where territories of grey wolves (*Canis lupus*) overlap management regimes in which they are protected from hunting and trapping on one side and subject to legal hunting and trapping on the other. For example, this situation occurs in and adjacent to Yellowstone National Park in Wyoming (D. Smith, pers. comm.), Algonquin Provincial Park in Ontario (Forbes & Theberge 1996), Banff National Park in Alberta (Callaghan 2002; Hebblewhite 2006), Kluane National Park in the Yukon Territory (Carey et al. 1994), and Denali National Park and Preserve in Interior Alaska (Mech et al. 1998). In each situation, there are multiple and potentially competing objectives of stakeholders, which include state and federal management agencies, private land owners, trappers, hunters, non-profit agencies, environmental advocates, and the general public. Additionally, there is often a great deal of uncertainty about system dynamics and the effects of management actions.

Wolf management in and adjacent to Denali National Park and Preserve (DNPP) exemplifies a complex management situation. All hunting and trapping (harvest) is prohibited in the area of the original Mt. McKinley National Park; however, subsistence and sport hunting and trapping are permitted in the Denali National Preserve and new park additions of Denali National Park, and trapping and hunting is legal on surrounding state lands. Wolves that live primarily within the park often range across the boundary of the park where harvest of wolves is legal (Mech et al. 1998). The National Park Service (NPS) is mandated to protect naturally functioning wildlife populations (United States 1916) and wildlife viewing opportunities (NPS 1986). Protection of wolves within the park provides for wolf viewing opportunities along the Denali Park Road for tens of thousands of visitors annually (Borg 2014). On state lands adjacent to DNPP, the Alaska Department of Fish and Game (ADF&G) is mandated to provide for consumptive (hunting and trapping) as well as non-consumptive (wildlife viewing) uses of wildlife such as wolves (ADF&G 2006). When there are perceived or real trade-offs between the objectives for consumptive and non-consumptive use of the same resources (i.e. wolves), conflicts may arise over the management of these shared resources.

Making decisions on how to best meet these objectives is not an easy or clear task when there are multiple conflicting objectives related to the management of a species. When combined with system dynamics that are relatively unknown and the response of the system to management actions is uncertain, the situation is even more complicated. Essentially, all management decisions must be made without perfect knowledge of system dynamics or the ability to precisely predict how the system will respond to actions. However, attempts should be made to make the best or optimal decision to meet objectives given the state of knowledge.

Structured Decision Making (SDM) and adaptive management are valuable tools that could be used to address issues of transboundary wolf management. In cases where the optimal solution to a management problem is not readily apparent, SDM provides a framework to elucidate the objectives, potential actions, and expected consequences of actions in order to identify the best solution given the current state of knowledge (Williams et al. 2002; Runge et al. 2013). The SDM process itself need not be complex but rather can be seen as "a formalization of common sense for decision problems which are too complex for informal use of common sense" (Keeney 1982).

SDM can incorporate uncertainty of the system dynamics and works well in situations where the management objectives are clear or can be clarified through problem decomposition (Clemen & Reilly 2001; Burgman 2005; Runge 2012). Adaptive management is the application of SDM to recurrent decisions, with a formal framework for dealing with the added complexity of how objectives, actions, and understanding of the system change over time (McCarthy & Possingham 2007). Adaptive management incorporates the ability to learn from actions by iteratively updating models of the system based on the system's response to actions in the previous time step (Conroy & Carroll 2009). In addition, adaptive management approaches allow for "double-loop" learning in which objectives and potential alternative actions are reassessed and readdressed over time.

In this introduction, I discuss how a SDM process could be applied to a one-time decision on regulation of harvest adjacent to DNPP by applying formal decision making steps (Runge 2012).

I discuss how data and analysis from chapters 2, 3, and 4 can be used to develop models of the system and its response to management actions. In the conclusion, I explain how results from previous chapters can be applied to models to help develop an optimal solution and address the final steps of the SDM process. Additionally, I explain how the framework could be used to address recurring decisions on regular or irregular intervals in an adaptive management approach.

For the purpose of this discussion, I make basic assumptions about the fundamental and means objectives of the primary land management agencies (NPS and the State of Alaska) based on regulatory statute. The fundamental objectives describe the ultimate goals of the decision maker and the means objectives represent intermediate goals to meet the fundamental objectives and should have measurable attributes and a performance criteria such as maximize, minimize or a threshold (Conroy & Carroll 2009).

These assumptions are not meant to cover the entire range of objectives, but serve as a framework for discussion of how to apply a formal decision making process to a complex problem. In addition, I consider a limited range of potential actions to address the means objectives. The limited range of potential actions is not intended to be an exhaustive treatment of management options. Most importantly, the assumptions and simplifications presented herein are not necessarily endorsed by the stakeholders or management agencies named.

1.2 Steps to a Structured Decision Making Process

1.2.1 Step 1. Define the Problem

The Wolf Townships are a rectangular region near the northwest corner of DNPP managed by the state of Alaska and surrounded on three sides by National Park land. The Wolf Townships are within Alaska State Game Management Unit (GMU) 20C (Figure 1.1). DNPP's 1986 General Management Plan (GMP) states that the Wolf Townships "*were recognized by Congress as important habitat for park caribou and wolf populations…[and] acquisition of these townships is needed to protect the natural ranges of these populations from incompatible development and sport hunting*" (NPS 1986).

Typically, two to four wolf packs in the eastern portion of DNPP occupy territories spanning both the Denali Park Road corridor and the Wolf Townships. These packs provide the majority of wolf sightings to an estimated 20,000 park visitors annually due to their proximity to the Denali Park Road (Borg 2014). However, wolves from these packs also use habitat in the Wolf Townships where they are subject to legal harvest. The NPS never acquired the Wolf Townships, but starting in the mid-1990's, advocates have lobbied for a "buffer zone" where trapping and hunting of wolves is prohibited to protect the packs that frequently live in the park but use these state lands (Haber 2002).

In 2000, the Alaska Board of Game (AKBOG) approved a 75 km^2 buffer zone in the Wolf Townships west of the Savage River where hunting and trapping of wolves were prohibited (Figure 1-1). In 2001 and 2002, the original buffer zone was expanded and second zone was added, increasing the protected area to 233 km^2. In March 2010, the NPS proposed an expansion of the existing buffer zone to the AKBOG with the objective of improving protection (i.e. reducing harvest) for wolves from commonly viewed packs (Hooge 2010). At the Interior Region Board of Game meeting on March 5, 2010, the AKBOG instead voted to remove the existing buffer zone. At the meeting, members of the AKBOG requested more information and research into the relationship between harvest of wolves in the Wolf Townships and wolf sightings within DNPP ("Unit 20 Wolf Closure Proposals" 2010).

1.2.1.1 Legal and regulatory context

Both the State of Alaska and the National Park Service have management mandates, regulations and policies directing the management of wildlife, including wolves. The State of Alaska mandate for natural resource management comes from the Alaska State Constitution, Section 8, "§ 2. General Authority — The legislature shall provide for the utilization, development, and conservation of all natural resources belonging to the state, including land and waters, for the maximum benefit of the people. § 3. Common Use — Wherever occurring in their natural state, fish, wildlife, and waters are reserved to the people for common use. § 4. Sustained Yield — Fish, forests, wildlife, grasslands, and all other replenishable resources belong to the State shall be utilized, developed, and maintained on the sustained yield principle, subject to preferences among beneficial uses."

Regulation of wolf harvest in the Wolf Townships is set by the Alaska Board of Game (AKBOG). The AKBOG is tasked with the dual mandate of conserving and developing Alaska's wildlife resources by Alaska Statute [AS 16.05.221 (b)] and is responsible for establishing open and closed seasons, areas for taking game, bag limits, and regulating means and methods of take [AS 16.05.255]. ADF&G is responsible for managing based on decisions made by the BOG [AS 16.05.020] with the functions to "manage, protect, maintain, improve, and extend the fish, game, and aquatic plant resources of the state in the interest of the economy and general well-being of the state".

The AKBOG's Wolf Management Policy also recognizes that "in some [...] areas, including national park lands, the Board also recognizes that non-consumptive uses of wolves may be considered a priority use. With proper management, non-consumptive and consumptive use are in most cases compatible but the Board may occasionally have to restrict consumptive uses where conflict among uses are frequent" ("Findings of the Alaska Board of Game 2011-185-BOG" 2011)

Management mandates for wildlife on the surrounding park lands were established by the 1916 Organic Act and the Alaska National Interest Lands Conservation Act (United States 1980), and summarized in the NPS Management Policies (2006). The 1916 Organic Act established the NPS with the dual mandate of conserving resources, such as wildlife, while also providing for visitor enjoyment of the resources (United States 1916). NPS Management Policies 2006 (Section 1.4.6) define park wildlife resources to include not only the species, but the "biological and physical processes that created the park and continue to act upon it…and native plants and animals…[and]…appropriate opportunities to experience enjoyment of the above resources, to the extent that can be done without impairing them".

In 1980, the passage of the ANILCA added over 43.5 million acres to the National Park system in Alaska, authorized subsistence harvest of wildlife in most of the new NPS lands, and provided for sport hunting and trapping in new Preserve lands. Thus, NPS mangers in Alaska are tasked with providing for subsistence and sport harvest on ANILCA lands. However, Section 815 of *ANILCA provides that these provisions should not be construed as permitting subsistence use "…inconsistent with the conservation of healthy populations of fish and wildlife, within a conservation unit, and the conservation of natural and healthy populations within a national park or monument…"*. Federal Subsistence Board regulations (50 CFR 100.4) clarifies and defines the conservation of healthy populations relative to subsistence harvest management in Alaska: "conservation of healthy populations of fish and wildlife means the maintenance of fish and wildlife resources and their habitats in a condition that assures stable and continuing natural populations and species mix of plants and animals in relation to their ecosystem, including the recognition that local rural residents engaged in subsistence uses may be a natural part of that ecosystem; minimizes the likelihood of irreversible or long-term adverse effects upon such populations and species; ensures the maximum practicable diversity of options for the future; and recognizes that the policies and legal authorities of the managing agencies will determine the nature and degree of management programs affecting ecological relationships, population dynamics, and the manipulation of the components of the ecosystem".

1.2.1.2 Scope of the decision

The scope of decision for this discussion is limited in the following ways: 1) geographically to the Wolf Townships, 2) to a subset of regulatory options including opening or closing a region to take (all means and methods) or restricting bag limits, and 3) to the frequency of a one-time decision (with discussion of recurrent decisions covered later). This problem deals with multiple objectives and uncertainty and is considered under the class of multiple objective tools with variable inputs (Table 1.1).

1.2.2 Step 2. Establish the Objectives

Fundamental and means objectives and associated constraints must be developed collaboratively through focused conversations between stakeholders (Kendall 2001). In practice, given the fundamentally opposing objectives of some stakeholders, defining a set of clear and mutually acceptable objectives may be difficult. Conflict resolution by a skilled facilitator may help distinguish ethical considerations, values, and regulatory responsibilities in order to clarify the fundamental and means objectives of each stakeholder in a way that would make the problem more tractable. However, considering only the state and federal management agencies as stakeholders for this discussion, the fundamental objectives of each agency can be considered relative to their management mandates, regulation, and policy.

Both state and federal management mandates, regulations, and policy directly address conservation and use of wildlife resources. The Alaska state constitution directs management of wildlife for the maximum benefit of Alaskans with consumptive use to be regulated through the sustained yield principle. NPS mandates are to 1) maintain and conserve wildlife populations and natural processes and 2) provide for visitor enjoyment. Federal mandates on preserve lands and ANILCA park additions are to provide for subsistence use, provided natural and healthy populations exist. In short, both federal and state management have mandates for maintaining wildlife populations and allowing for their use. However, a fundamental difference is that state mandates and policy allow for, and at times require, active management of wildlife populations, while the federal mandates are to allow for natural processes and fluctuations to dominate the system.

For this discussion, I focus on defining objectives related to the primary uses of wolves in and adjacent to DNPP. Primary uses of wolves can be classified as consumptive (primarily hunting and trapping for fur) or non-consumptive (primarily wolf viewing). I describe two fundamental objectives related to each use with suggested means objectives, measurable attributes, and performance criteria:

Objective for consumptive use

- **Fundamental:** Provide for consumptive uses of wolves through trapping and hunting opportunities in the Wolf Townships, subject to the sustained yield principle.
- **Means:** Sufficient area, open seasons, and bag limits such that Alaskans have opportunities to hunt and trap wolves.
- **Measurable attribute:** Number of wolves sealed per unit of effort per active (Alaskan) trapper/ hunter, W_h. Harvesting a wolf is challenging, unpredictable, and subject to random chance, therefore a measure of wolf harvest opportunity, W_o, such as number of active users, number of traplines maintained, etc., may be an appropriate measurable attribute for this objective.
- **Performance criteria:** Maximize or threshold

Objective for non-consumptive use

- **Fundamental:** Provide for non-consumptive uses of wolves through wolf viewing opportunities (which occur mainly along the Denali Park Road).
- **Means**: Maintain wolf packs that overlap the road (eastern packs), numbers of wolves in those packs, and the individual behavior of wolves in those packs that allow for wolf viewing opportunities
- **Measurable attribute:** Proportion of trips along the Denali Park Road to Eielson Visitor Center that see a wolf during a trip, P_s
- **Performance criteria:** Maximize the potential for visitors to view wolves in DNPP or develop a threshold

An alternative and perhaps more useful approach, would be to state the fundamental objective as a combined objective to provide for both consumptive and non-consumptive use. However, the two primary means objectives may remain unchanged. In this circumstance, there may be trade-offs such that actions that are beneficial for one means objective are not equally beneficial or are detrimental to the other means objective. There are two potential approaches for dealing with this circumstance (Conroy & Carroll 2009). The first approach would be to assign a weight to each objective and select the decision that optimizes some combined value. Higher weights for one objective over another would favor making decisions supporting the highly weighted objective. Another alternative is to restrain decision making to maintain one objective within acceptable bounds while maximizing the second objective. The "acceptable bound" in this case is essentially a utility threshold. The utility threshold is a component of the management objective, at which a small change in the performance criteria yields a substantial changes in the management outcome (Martin et al. 2009). In this example, an objective may be to maintain a reasonable chance for park visitors to observe the wolves, such that the probability of wolf sightings are maintained above a threshold, τ. The value for τ would represent a subjective value, and need to be determined by stakeholders during the SDM process.

Combined Objective

- **Fundamental:** Provide for non-consumptive uses of wolves through wolf viewing opportunities and allow for consumptive use of wolves when objectives for sightings are met
- **Means**: Maintain wolf viewing opportunities above a threshold while allowing or maximizing wolf harvest opportunities
- **Measurable attributes:** Proportion of trips along the Denali Park Road to Eielson Visitor Center that see a wolf during a trip (P_s), action of opening or closing the Wolf Townships (A), and number of wolves harvested in the Wolf Townships (W_h) and/or harvest opportunities (W_o)

- **Performance criteria:** Maintain *P* above threshold for wolf sightings (τ). Maximize or allow wolf harvest or harvest opportunities.

There are additional objectives not directly related to consumptive and non-consumptive uses of wolves themselves. In addition to providing for visitor enjoyment and providing for harvest, there are NPS mandates to maintain natural processes and provide for healthy and naturally functioning wildlife populations. It is an ongoing challenge and beyond the scope of this discussion to develop means objectives and quantifiable goals, such as minimize or maximize, or a numeric threshold, that fully encompass the broad wildlife management mandates and stewardship goals of the NPS. Through active research and the long term monitoring programs in the parks, NPS managers are continuing to define and understand not only the natural range of population fluctuations, but also how wildlife functions in a naturally regulated ecosystem and what defines the range of natural processes (Hilderbrand et al. 2013). Chapter 2 adds to this growing body of work, improving our understanding of how natural and anthropogenic sources of mortality of reproductive wolves (breeders) influence wolf social structure through pack stability, reproduction, and population growth rates.

In addition to the non-consumptive value of wolves for wolf viewing opportunities, the NPS is mandated to preserve ecosystems and associated species, as a result NPS lands act as 'living laboratories' (Grinnell & Storer 1916; Shea 2015). The DNPP wolf population has a long history of research and relative protection from harvest (Murie 1944; Mech et al. 1998; Adams et al. 2008). This makes the DNPP wolf population unique worldwide and valuable for continuing research (Borg & Burch 2014; Borg et al. 2015). Thus there are additional objectives relating to maintaining a wolf population dominated by natural processes and natural mortality to the Park Service and scientific community.

There are also objectives of the State of Alaska relative to management of wolves not directly addressed by the consumptive and non-consumptive uses of wolves themselves. When the objective is to manage ungulate populations for high levels of human harvest, state statutes, and the Intensive Management Law allow for reducing wolf populations to meet these objectives [AS 16.05.255 (e)-(g) and (j)-(k)]. In these cases, the objective for wolf management is not related directly to the consumptive use of wolves themselves but in reducing wolf numbers to meet the objective for consumptive use of the identified ungulate population. This additional objective applies in other areas of the state, but does not currently apply to the Wolf Townships adjacent to Denali National Park.

1.2.3 Step 3. Define the Potential Actions

Stakeholders, agency representatives and scientists should collectively create a list of potential actions to achieve the fundamental and means objectives. Previously, the AKBOG prohibited hunting and trapping of wolves within an identified region to address the objective of reduced wolf harvest of specific packs that contribute to wolf sightings. Other areas in North America provide examples of potential actions implemented to meet management objectives.

The vast majority of wolf packs in the eastern portion of Algonquin Provincial Park follow migrating white-tailed deer out of the park where the wolves were subject to harvest, which resulted in a declining wolf population (Forbes & Theberge 1996; Theberge & Theberge 2004).

Due to concerns regarding the wolf population decline, a 10-kilometer buffer area where harvest of wolves was prohibited was established outside of the park (Theberge & Theberge 2004). In Kluane National Park, the desire to preserve a naturally-regulated wolf population led to the creation of a buffer zone outside of the park designed to protect wolves that primarily resided within the park (Carey et al. 1994). Conversely, there have been no closures or reduced harvest levels adjacent to Banff National Park, as the wolf population within Banff National Park is considered a source population (Thiessen 2007) and harvest of wolves from packs residing primarily in the park is frequent along the park boundaries (Callaghan 2002; Hebblewhite 2006). The State of Montana established small hunting units with reduced quotas for wolves adjacent to Yellowstone National Park, to reduce the risk of harvest for wolves that primarily live within the boundaries of the park (D. Smith pers. comm., Montana Fish Wildlife and Parks 2013).

Often the initial range of options considered is unnecessarily narrow, constrained by perception of feasibility and considerations of logistics (Runge 2012). Identifying buffer zones or sensitive areas adjacent to protected areas is a common theme for potential actions to meet the objectives of reducing harvest of wolves residing primarily within protected areas. Other potential options include a gradient of harvest levels surrounding protected areas with reduced quotas or bag limits adjacent to the park, or a numerical limit based on population estimates prior to the harvest season.

The following list of alternative actions is limited to actions previously proposed by stakeholders. However, in order to facilitate a discussion of how to develop models and make decisions on the best action, it helps to have some actions to consider. For the subsequent steps, I focus on the two alternative actions in italics.

<u>Alternative actions</u>

- *Open Wolf Townships to harvest (restrained only by open season and method of take)*
- *Completely close Wolf Townships to harvest*
- Partially close Townships
  - Identify sensitive or "high risk" areas and completely close identified areas to harvest
  - Restrict methods and means: i.e. reduce bag limits or method of take

1.2.4 Step 4. Consequences

The purpose of this step is to develop models that link the actions to outcomes. This requires 1) clearly stating the objective of the modeling effort and how the model will be used in the management context and 2) developing a model specific for its intended use. Model development includes a careful consideration of the potentially important variables to include in the model. The intent is to model with the management action in mind, making the model only as complex as needed to meet the purpose. The model need not explicitly incorporate all ecological processes, and abiotic and biotic variables. However, variables considered important to the system should be incorporated as a source of variation in the model.

There are multiple forms of uncertainty incorporated in models. These include environmental variation, partial controllability (the extent to which management actions are implemented completely), partial observability (accounting for imperfect observation system), and structural uncertainty (the uncertainty related to how system dynamics respond to management actions).

During the modeling process, the focus is on reducing or accounting for structural uncertainty (Conroy & Carroll 2009). Structural uncertainty can be represented through a discrete set of alternative models of system response (Williams et al. 2002). In the conclusion I discuss how adaptive management can be used to resolve structural uncertainty.

The objective for this modeling effort is to link the management action, *A,* of opening or closing the Wolf Townships to harvest to the objectives for consumptive and non-consumptive use of wolves. This requires using a scientific approach and developing mathematical models that describe system behavior, the relationship between management actions and outcomes, and associated measures of confidence in the models (Williams et al. 2002; Nichols & Williams 2006). In the subsequent chapters, I, along with co-authors and collaborators, used data from Denali National Park and Preserve (DNPP) and Yellowstone National Park (YNP) in order to develop models of the system incorporating key variables, and provide estimates of the response of wolf social structure, population dynamics, and sightings to harvest adjacent to these protected areas.

In Chapter 2, I look at how harvest of breeding wolves may influence pack persistence, den site tenure and reproductive success, which may all influence wolf sighting rates along the Denali Park Road. In Chapter 3, I take a broad look at how harvest of wolves adjacent to two National Parks in North America influences wolf sightings within the parks. We analyze data on wolf sightings, pack sizes, den site locations, and harvest adjacent to DNPP from 1997-2013 and YNP from 2008-2013 to evaluate the relationship between harvest of wolves and wolf viewing opportunities. In Chapter 4, I use spatially-explicit data on wolf sighting locations from 1997-

2013 to evaluate factors that influenced the probability of a wolf being near the road and the detectability of a wolf in a given section of road. Our spatially explicit model partitions variation in sightings due to den site location and pack size along the road to provide a quantitative measure of the relative impact of these factors.

In Chapter 5, I take a look at how the results from these studies provide models of the system and response to management actions. I incorporate the models into a utility function, which quantifies the benefit obtained by implementing a management action (Williams et al. 2002; Martin et al. 2011) and discuss incorporating structural uncertainty into the models of the system. I address the remaining steps in an SDM process: developing and optimal solution and implementing the action. Finally, I address how an adaptive management approach could be applied with the additional steps of monitoring and learning.

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1.4 Figure

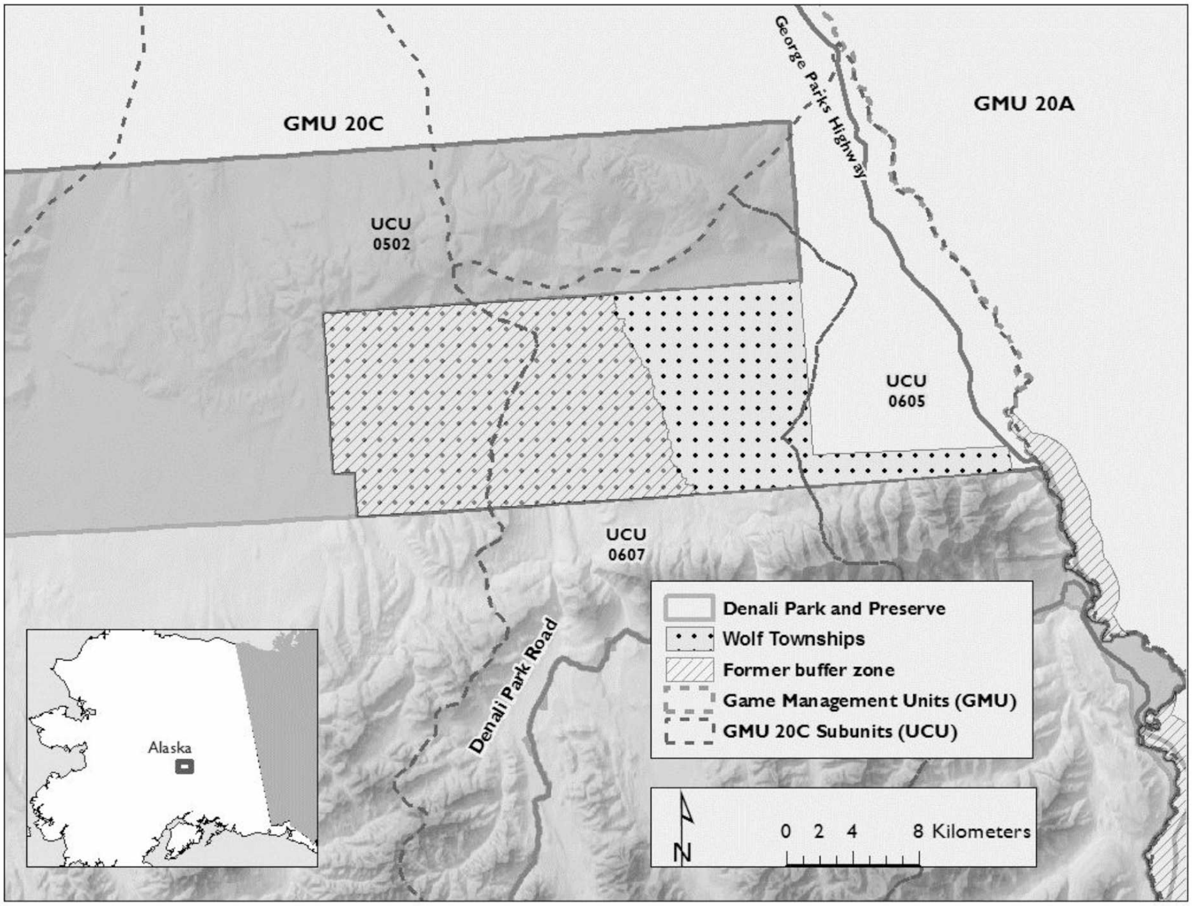

Figure 1.1. Map of the northeast corner of Denali National Park and Preserve in interior Alaska, USA. Alaska State Game Management Units and Subunits are shown, as well as the Wolf Townships, adjacent to the DNPP boundary, as defined in the DNPP 1986 General Management Plan. Areas of a former "buffer zone", in place from 2000- 2010, prohibiting the trapping and hunting of wolves adjacent is shown in diagonal hashes.

1.5 Table

Table 1.1. Class of problems for Structured Decision Making

	No Uncertainty	With Uncertainty
Single Objective	Management Science, optimization tools	Classic decision analysis; Decision trees
Multiple Objective	Multi-attribute tradeoff tools and complex optimization	Multiple objective tools with variable inputs

Chapter 2

Impacts of Breeder Loss on Social Structure, Reproduction and Population Growth in a Social Canid[1]

2.1 Abstract

The importance of individuals to the dynamics of populations may depend on reproductive status, especially for species with complex social structure. Loss of reproductive individuals in socially complex species could disproportionately affect population dynamics by destabilizing social structure and reducing population growth. Alternatively, compensatory mechanisms such as rapid replacement of breeders may result in little disruption. The impact of breeder loss on the population dynamics of social species remains poorly understood. We evaluated the effect of breeder loss on social stability, recruitment and population growth of grey wolves (*Canis lupus*) in Denali National Park and Preserve, Alaska using a 26-year dataset of 387 radiocollared wolves. Harvest of breeding wolves is a highly contentious conservation and management issue worldwide, with unknown population-level consequences. Breeder loss preceded 77% of cases (n = 53) of pack dissolution from 1986 to 2012. Packs were more likely to dissolve if a female or both breeders were lost and pack size was small. Harvest of breeders increased the probability of pack dissolution, likely because the timing of harvest coincided with the breeding season of wolves. Rates of denning and successful recruitment were uniformly high for packs that did not experience breeder loss; however, packs that lost breeders exhibited lower denning and recruitment rates. Breeder mortality and pack dissolution had no significant effects on immediate or longer-term population dynamics.

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[1] Borg, B. L., S. M. Brainerd, T. J. Meier, and L. R. Prugh. 2015. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. Journal of Animal Ecology 84:177–187.

Our results indicate the importance of breeding individuals is context-dependent. The impact of breeder loss on social group persistence, reproduction, and population growth may be greatest when average group sizes are small and mortality occurs during the breeding season. This study highlights the importance of reproductive individuals in maintaining group cohesion in social species, but at the population level socially complex species may be resilient to disruption and harvest through strong compensatory mechanisms.

2.2 Introduction

Many species have evolved complex social systems in which only a few individuals within a social group reproduce. For example, reproduction among subordinates can be suppressed or delayed in eusocial animals (e.g Wilson 1971), a number of bird species (Arnold & Owens 1998), and in social carnivores (Kleiman 1977; MacDonald 1983). The importance of specific individuals may be especially variable for social species that exhibit reproductive suppression of subordinates, because this suppression creates skewed heterogeneity in the reproductive value of individuals (e.g. Stahler *et al.* 2013). Population models are particularly sensitive to variation in reproductive performance among individuals or age classes (Kendall et al. 2011; Lindberg et al. 2013). However, the impact of reproductive individuals on the population dynamics of species with complex social structure remains poorly understood. Mortality of reproductive individuals may disproportionately affect population growth, unless other reproductively viable individuals are able to take their place with little disruption. In this paper, we examine the effects of mortality of reproductive individuals ("breeders") on grey wolf (*Canis lupus*) social structure, reproduction, and population growth using a 26-year dataset from Denali National Park and Preserve (DNPP) in interior Alaska.

As long-lived canids with a family-based social system (Mech 2000), grey wolf pack and population dynamics may be highly sensitive to the fate of breeders. Breeders and/or dominant individuals play an important role in pup survival (Brainerd et al. 2008), hunting behaviour and efficiency (Sand et al. 2006; MacNulty et al. 2011) and interpack competitions (Cassidy 2013). However, early models of wolf population dynamics ignored this source of individual variation (Soule 1980, 1987; Keith 1983; Fuller 1989; Boyce 1990) and generally failed to predict dynamics accurately (Fuller et al. 2003). More recent models have accounted for wolf social structure (Haight & Mech 1997; Vucetich et al. 1997; Haight et al. 1998, 2002; Cochrane & Fitts 2000; Fuller et al. 2003), but we still lack an adequate understanding of how the loss of breeding individuals affects pack and population dynamics. Better understanding of how social structure relates to population viability and the fitness of wolves has been identified as a priority for wolf management and conservation (Stenglein et al. 2011).

There is growing recognition of the importance of explicitly considering sources of heterogeneity in harvest management of vertebrates (Lindberg et al. 2013), because harvest of individuals with high reproductive value can have a greater effect on population dynamics than harvest of individuals with low reproductive value (Kokko 2001; Hauser et al. 2006). Understanding the consequences of breeder mortality on wolf population dynamics is increasingly important as wolves recolonize areas of North America and Europe (Wabakken et al. 2001; USFWS 2007; Wydeven et al. 2009). Wolves have recently been delisted from the Endangered Species Act

(ESA) in several of the United States and are currently subject to hunting and trapping in regions of the United States and Europe. Scientists, policy makers and the public continue to debate what constitutes a sustainable level of harvest for these wolf populations. Progress in resolving this debate is hindered in part because the effect of breeder loss on the population dynamics of social species such as wolves remains largely unknown.

Wolf populations have typically been viewed as highly resilient to harvest (reviewed in Fuller *et al.* 2003, Adams *et al.* 2008), but recent studies suggest wolf populations may be less resistant to harvest impacts than previously thought (Smith *et al.* 2010; Creel & Rotella 2010; Sparkman, Waits & Murray 2011; but see Gude *et al.* 2012). We hypothesize that the level of sustainable wolf harvest may depend on the breeding status of harvested wolves and the timing of harvest. For example, removal of a breeding female, especially if timed during the breeding season, may induce reproductive failure for the pack that year (Brainerd et al. 2008; Stahler et al. 2013). If individuals of high reproductive value, such as breeding wolves, are selectively harvested or disproportionately vulnerable to harvest, the level of harvest that can occur without population level impacts may be lower than commonly accepted thresholds (Lindberg et al. 2013).

In a previous analysis of breeder loss in wolves, Brainerd et al (2008) found that pack fate (i.e., whether a pack persisted or dissolved) depended on pack size prior to breeder loss and whether one or both breeders died. However, the effect of breeder loss on population growth was not assessed. Additionally, the importance of other factors that could moderate the effects of breeder loss on pack maintenance or population growth, such as the timing and cause of mortality, remains unknown.

We evaluated the impacts of anthropogenic and natural mortality of breeders on wolf pack maintenance, reproduction, and population growth using data on 387 radiocollared wolves in 70 packs. We hypothesized that the sex of breeder lost, pack size prior to loss, and the timing of loss would influence pack fate, denning behaviour, pup recruitment, and population growth. Anticipating high overlap between anthropogenic mortality and the breeding season, we also expected cause of death to affect pack fate. We hypothesized that loss of breeders and packs could reduce population growth primarily by reducing the reproductive capacity of the population (Mech et al. 1998; Fuller et al. 2003). Alternatively, breeders could be replaced with negligible impact or even a positive effect on population growth. Pack dissolution may create opportunities for existing packs to usurp old territories, allow new pairs to set up territories where packs have dissolved, or packs may subdivide existing wolf territories with the effect of increasing wolf densities locally (Ballard & Stephenson 1982; Meier et al. 1995; Mech et al. 1998; Mech & Boitani 2003).

2.3 Methods

2.3.1 Study Area

The study area encompassed approximately 17,270 km^2 of wolf habitat primarily north and west of the Alaska Range in and adjacent to DNPP (Fig. 2.1). The eastern region of DNPP contains habitat patches of high alpine, open gravel river bars, and willow-lined creeks. The western region of the park is more homogenous, dominated by relatively flat, lowland black spruce (*Picea mariana*) forest and long meandering rivers and wetlands. The diversity of habitat types in the eastern region of the DNPP supports caribou (*Rangifer tarandus*), Dall's sheep (*Ovis* *dalli*), and moose (*Alces alces*) populations. The western lowlands support lower densities of ungulates (primarily moose), and salmon are an important food source for wolves in this region (Mech et al. 1998; Adams & Roffler 2009; Owen & Meier 2009; Adams et al. 2010).

2.3.2 Data Collection

Wolf population monitoring efforts in DNPP and use of radiotelemetry for tracking and monitoring packs began in 1986 (Mech et al. 1998). From 1986 to 2012, 387 individual wolves were radiocollared with very high frequency (VHF) collars (Meier 2011). From 2003 to 2012, 30 of the VHF collars were equipped with GPS (Telonics, Mesa, CA) which provided daily locations uploaded through the Argos satellite system (Meier et al. 2009). Wolves were immobilized by darting from helicopters and collared following protocols described in Meier (2009).

Researchers gathered annual wolf population and composition data in early and late winter (November-December and February-March respectively). Radiocollared wolves were located by VHF signal from fixed-wing aircraft. Approximately 10 to 20 wolf packs were monitored annually in the study area and efforts were made to maintain collars on two or more individuals in each pack whose home range was mostly within DNPP boundaries. Wolf location, number of pack members, pelt colours, and estimated age classes (if distinguishable) were recorded. Observers also recorded detailed information on mortality, den site location/use, and pack affiliation (Mech et al. 1998; Meier et al. 2009).

Wolf mortalities were noted during aerial tracking and observation and through weekly GPS data checks. Cause of death was determined through a field necropsy or by wildlife veterinary staff at the University of Alaska Fairbanks (UAF) or the Alaska Department of Fish and Game (ADF&G). When carcasses were too decomposed to determine cause of death or both lab and field evidence were inconclusive, cause of death was recorded as “unknown natural”.

All areas outside of the DNPP boundary were open to hunting and trapping under state regulation, with open seasons and bag limits (i.e., the number of wolves that could be harvested per person) managed by ADF&G. In Game Management Units (GMU) 20A and 20C adjacent to the park’s boundaries, the hunting season was August 10 – April 30 from regulatory year 1996-1997 through 2005-2006 and extended until May 31 starting in 2006-2007. The bag limit was 10 wolves until 2001-2002 and was then decreased to five wolves per season. The wolf trapping season spanned November 1– April 30 in GMUs 20A and 20C, with no bag limits for either unit. Subsistence and sport hunting and trapping were permitted in the Preserve and new park additions of DNPP, but all hunting and trapping was prohibited in the area of the original Mt. McKinley National Park (Fig.2.1).

2.3.2.1 Pack Size and Pack Fate

We examined the size and fate of all packs monitored in DNPP from 1986-2012. Pack size during spring and fall was defined as the maximum count observed during surveys within each season. We defined pack formation as occurring the season (spring or fall) and year of the first pack count recorded for the associated pack name. We defined pack dissolution as the reduction of a pack of ≥3 wolves to zero or one wolf the subsequent season. Because the exact fate of remaining pack members was often unknown (i.e., they may have died, dispersed, or remained present but undetected), the concept of pack persistence in this study is analogous to "apparent survival" in capture-mark-recapture studies (Lebreton et al. 1992). Pack life span was calculated as the number of years from pack formation (or from the start of monitoring) to pack dissolution.

For analyses of breeder loss effects on pack maintenance and reproduction, we included only established packs that were monitored or known to exist for ≥1 year. Packs were considered to have dissolved following breeder loss if the dissolution occurred the season following or during the same season as the breeder loss. In the absence of collars, observers used colour composition and number of associated individuals or distinguishing features to determine if individuals or groups found within the former territory were original pack members, neighbouring pack members or previously unknown wolves. Pack dissolution rate for the population was calculated as the number of packs dissolving in a year divided by the total number of packs monitored.

2.3.2.2 Breeder Loss

Biologists generally targeted dominant members of packs for collaring by observing the behaviour of pack members during aerial tracking and collaring operations (Meier et al. 2009), but subordinate wolves were sometimes collared. The breeding status of individuals was determined through observation of leadership behaviour, attendance at den sites, observation of nursing pups (for females) during aerial tracking, and/or through testes and nipple measurements during collaring (Mech 1999, 2000; Peterson et al. 2002; Meier et al. 2009). However, breeding status or dominance status was not recorded for all wolves in the dataset.

We used a heuristic method to identify likely breeders from the dataset of all collared wolves in DNPP from 1986-2012. We censored wolves from our dataset that were: 1) < 2-years-old when they died, 2) dispersing or had dispersed out of the study area at the time of death, 3) classified as pups or yearlings when captured, unless these were later classified as "alpha", "breeder" or "paired" in the capture or aerial tracking data, or 4) had an unknown fate due to collar failure or dispersal. We performed additional review to corroborate our method of breeder classification in two ways: 1) we compared wolves identified as breeders by our method to a subset of breeders from 1986 to 1993 identified and used for analysis by Brainerd et al. (2008), and 2) classification of individuals monitored from 1995 to 2012 was verified by reviewing capture, mortality and aerial tracking information from the corresponding time period.

We classified breeder mortality as occurring in one of four equal length seasons. Season breakpoints were determined primarily based on wolf breeding cycles in interior Alaska. Wolves in DNPP typically come into estrus in March (Mech et al. 1998) and give birth in early May following a two month gestation (Hayssen & van Tienhoven 1993). There is a prolonged period of proestrus in grey wolves of about six weeks (Asa & Valdespino 1998) during which the mated pair spends time together coordinating their activity, and this period appears important for the formation and maintenance of the pair bond (Mech & Knick 1978; Rothman & Mech 1979). We therefore defined spring as February-April (breeding season), summer as May-July (pup-rearing season), fall as August-October, and winter as November-January. Cause of mortality was classified as natural (including intraspecific strife, starvation, accident, and unknown natural causes) or anthropogenic (trapped, shot, vehicle strikes or capture-related mortality). We evaluated the proportion of natural and anthropogenic mortalities of identified breeders that occurred within each season to assess seasonal patterns in cause of mortality.

For analysis of the probability of pack maintenance, we censored cases of breeder loss where 1) pack persistence was unknown following the loss of the breeder, 2) pack size prior to the loss of the breeder was unknown, 3) packs were monitored or existed for less than a year after wolves were collared, or 4) groups were identified as pairs rather than reproductive packs.

2.3.2.1 Recruitment and Den Fidelity

We examined cases of pack denning and recruitment from 1997 to 2012 for packs in the eastern region of DNPP (Fig. 2.1). Data on den site use and reproduction prior to 1997 was not accessible and therefore excluded from analysis. We collated locations from collared wolves by pack and created minimum convex polygons that bounded the territory for each wolf pack by year using the program ArcGIS 10.0 (Esri, Redwoods, CA). Packs were designated as belonging to the eastern or western region when the centre of the pack territory was located within the corresponding geographical region. DNPP wolf management plan objectives require closing areas around known den sites to hikers (National Park Service 2007). Thus, den site locations and use were closely monitored for wolf packs in the eastern region, which includes the areas of higher potential backcountry recreational use in DNPP. This close monitoring provided more accurate data on denning status and presence of pups in fall (recruitment) in the eastern region than in the western region.

Wolf packs were recorded as having successfully reproduced using one of three methods: 1) one or more visual observations of attendance at known or suspected den sites during the denning season (April through mid-August), 2) clusters of GPS points at a known or suspected den locations, or 3) detection of pups during aerial tracking flights. Denning status was assumed to be an indication of reproduction. Early denning behavior that failed to produce surviving pups may have been missed and classified as no known denning or unknown denning status.
Den site fidelity was recorded for each pack each year; packs that used the same den in year $n+1$ as in year n had fidelity whereas packs that changed locations between years did not. Den site tenure was defined as the number of consecutive years that a pack used the same den site.

Recruitment was categorized as successful or failed based on: 1) visual observations of pups during the summer or early fall counts when pups were easily distinguished from adults, or 2) an increase in estimated pack sizes from spring to fall. We censored cases with increases in pack size of one or two individuals without corresponding visual observation of pups, because these cases could be explained by possible immigration or adoption of individuals. Recruitment was recorded as failed when packs either did not den or pups were never observed and pack size did not increase as described. We censored cases of newly formed pairs (those that formed after or during the breeding season) in our analysis because newly formed pairs have a lower probability of successful reproduction and recruitment (Mech et al. 1998). We evaluated denning and recruitment for packs that experienced breeder mortalities that occurred during the breeding season, pup-rearing season or the prior winter. Cases where packs dissolved or were maintained following breeder loss were both included.

2.3.2.1 Statistical Analyses

Factors affecting pack maintenance following breeder loss. We hypothesized that pack maintenance would depend on the sex of breeder lost (male, female or both), pack size prior to breeder loss, season of breeder loss, and cause of mortality (anthropogenic or natural). We used the glm function in Program R (R Core Team 2014) to create generalized linear models with all four main effects and all nested models with no interaction or higher order terms (n = 15 models). We used Akaike information criterion corrected for small sample sizes (AIC_c) to rank models, and we calculated pseudo-R^2 to estimate explained variance (Veall & Zimmerman 1992). We used the modavg function in R package AICcmodavg (Mazerolle 2013) to obtain model-averaged parameter estimates for factors that were included in models with ΔAIC <4 (Burnham & Anderson 2002). For ease of interpretation of parameter estimates, we transformed the parameter estimates (β) into odds ratios such that the odds ratio was equal to e^{β}.

Effect of breeder loss on recruitment and den site fidelity. We used chi-squared tests of independence to test the hypotheses that breeder loss (loss of a male, female or both breeders) would 1) reduce rates of denning, 2) reduce successful recruitment, and 3) reduce den site fidelity.

Effect of breeder loss on population growth. The annual population growth rate, or finite rate of increase (λ), for year n was calculated as the spring population size in year $n+1$ divided by the spring population size in year n. Breeder mortality rate was calculated as the number of breeder mortalities from May 1 in year n to April 30 in year $n+1$, divided by two times the number of packs monitored in year n (to correspond to the estimated number of breeders in the population).

If a different number of packs were observed during the spring and fall population counts, the larger number of packs was used as the number of packs monitored during the year.

We examined the relationships between the breeder mortality rate and λ and between the pack dissolution rate and λ using linear regression. To examine the immediate and longer-term effects of breeder loss on population growth, relationships were modelled with and without a one-year time lag (i.e., effect of breeder mortality or pack dissolution in year n on the population growth rate in $n+1$). We censored the first three years of the study (1986-1988) due to the low number of packs that were tracked during those years.

2.4 Results

2.4.1 Pack Fate and Breeder Loss

From 1986 to 2012, wolves from 70 packs were monitored in DNPP (Table S2.1). Eight packs were censored because the pack fate was unknown due to limited monitoring, and 9 packs continued to be monitored at the end of the study period in 2012. Of the remaining 53 packs, there were 41 cases (77%) where breeder mortality preceded or coincided with the end of the pack, and 12 cases (23%) where either there was no breeder mortality prior to the end of the pack or breeder mortality was not documented.

We identified 163 cases of breeder mortality from 1986-2012. Our heuristic method correctly identified 27 of the 31 (87%) collared breeder mortalities from 1986 to 1993 identified by Brainerd et al. (2008). The four breeders that were missed by our selection were all individuals that were captured as pups (n = 2) or yearlings (n = 2) and later became breeders in their own pack (n = 2) or dispersed and became breeders in another pack (n = 2). Some breeders that were collared as pups or yearlings and later became breeders may be missing in our dataset if there was no corresponding note in the capture, mortality or aerial tracking data to indicate that the individual was a breeder.

After censoring (see Methods), we used 94 cases of breeder loss for our analysis of factors affecting pack fate (Table 2.1). We found that packs dissolved the season following breeder loss in 31 cases (33%) and remained intact following breeder loss in 63 cases (67%). Roughly equal proportions of yearly breeder mortality occurred in spring, fall and winter, with 29.8%, 29.8%, and 30.9% of mortalities occurring in these seasons, respectively. The remaining 9.5% of mortalities occurred during summer. Anthropogenic mortality represented 11% and 14% of total mortality during summer and fall, respectively, while in spring and winter anthropogenic mortality represented 39% and 34% of total mortality (Fig. 2.3). Harvest (trapping or hunting) was the source of 21 out of 26 (81%) of anthropogenic mortalities; the other 5 cases (19%) were capture-related.

Sex of lost breeders and pack size were the most important predictors of pack persistence following breeder mortality (Table 2.2). A pack was 14.9 times more likely to persist if only the male was lost and 3.4 times more likely to persist if only the female was lost compared to cases where both breeders were lost (Table 2.3). The odds of a pack dissolving decreased with pack size (Fig. 2.2). The probability of pack maintenance was < 0.5 if both breeders were lost in packs with ≤ 11 members or a female was lost in packs with < 6 members.

Cause and season of mortality were included in the top-ranked models (ΔAIC_c <2). The model-averaged odds ratios indicated the probability of pack persistence was 1.6 times higher when breeders were lost due to natural causes rather than anthropogenic mortality, and mortality that occurred in spring or winter decreased the probability of pack maintenance while mortalities that occurred during the summer increased the probability of pack persistence relative to mortalities that occurred in the fall (Table 2.3).

2.4.2 Breeder Loss and Population Growth

Breeder loss did not affect population growth in the current year, λ_n, or the following year, λ_{n+1} (λ_n: β = -0.64, $F_{1,21}$ = 1.87, p = 0.19, R^2 = 0.08, n = 23, Fig. 2.4a; λ_{n+1}: β = 0.23, $F_{1,20}$ = 0.23, p = 0.63, R^2 = 0.01, n = 22, Fig.2.4b). Pack dissolution had a marginal negative effect on population growth in the current year but no effect the following year (λ_n: β = -0.81, $F_{1,21}$ = 3.10, p = 0.09, R^2= 0.13, n = 23, Fig. 2.4c; λ_{n+1}: β = 0.71, $F_{1,20}$ = 2.11, p = 0.16, R^2 = 0.10, n = 22, Fig. 2.4d).

2.4.3 Recruitment and Den Fidelity

We determined pack denning status in 79 cases from 1997 to 2012. Packs denned in 72 cases (91%) and successfully reared pups in 63 of the 72 cases (88%; Table 2.4). For packs that did not lose breeders, rates of denning (96%, n = 54) and successful recruitment (94%, n = 52) were uniformly high. Packs that experienced breeder loss had significantly lower denning and recruitment rates than packs that did not experience breeder loss (denning: 80%, $\chi 2$ = 3.896, df = 1, P = 0.049, n = 79, recruitment: 70%, $\chi 2$ = 5.697, df = 1, P = 0.017, n = 72).

Breeder loss did not significantly affect den site fidelity ($\chi^2 = 1.90$, df = 1, $P = 0.17$, $n = 48$). Packs used the same den site in consecutive years in 20 of 37 cases (54%) when no breeder loss occurred between breeding seasons and in 10 of 16 cases (63%) following breeder loss when the pack continued following the breeder loss (Table 2.4). Packs used the same den for an average of three consecutive years (range = 1-13 years, n = 10 packs).

2.5 Discussion

Our results show that the mortality of breeding individuals in social groups can often lead to social group dissolution, but population growth can be resilient to the effects of breeder mortality. Although breeder loss preceded or coincided with most documented cases of wolf pack dissolution, packs remained intact in approximately two of every three cases of breeder loss (Table 2.1). Population growth rates were largely unaffected by breeder loss and pack dissolution despite reduced reproductive rates, indicating that strong compensatory mechanisms can reduce the negative impacts of breeder loss in socially complex species such as wolves.

While the effects of breeder loss on wolf population dynamics in DNPP appear to be minor in general, our findings indicate the availability of replacement breeders and timing of mortality can moderate the consequences of breeder loss. The importance of the cause and timing of mortality indicates the value of reproductive individuals in social species may be context-dependent and characterized by strong seasonal heterogeneity. Our results suggest that reproductive value of individuals increases as they approach parturition such that mortality of breeders during this time can destabilize social groups and lead to reproductive failure. The effects of variable reproductive value among age classes can alter population dynamics (Francis et al. 1992), and our results imply that seasonal variation in addition to reproductive status can affect social and population dynamics.

Although direct causes of pack dissolution were generally not known, dissolution followed or coincided with the loss of one or both breeders in at least 77% of the cases. This rate was likely underestimated because not all breeders were collared, and thus not all breeder mortality events were observed. Breeders may thus contribute disproportionately to the social stability of groups (Mech & Boitani 2003) in addition to having high reproductive values. The importance of breeders in this socially structured species highlights the need to explicitly consider the effects of harvest of these individuals, especially when harvest overlaps the breeding season.

Anthropogenic mortality has been shown to impact social structure in grey wolves, such that harvested populations tend to have smaller packs (Ballard et al. 1987) and harvest may reduce genetic relatedness (Rutledge *et al.* 2010 but see Lehman *et al.* 1992). We found that packs were less likely to be maintained when breeders were killed by humans than when mortality resulted from natural causes. Although this finding supports previous research, it is still surprising given that the cause of mortality should not necessarily affect pack fate per se. We suspect the timing of anthropogenic mortality in relation to breeding season may partially account for the observed effects on pack fate. Anthropogenic harvest mortalities were concentrated in spring breeding and winter pre-breeding seasons (Fig. 2.3). Mortalities during spring in particular leave little time for replacement of breeders and may have a disproportionate effect on pack persistence. Our results indicate that harvest of breeding wolves has the potential to impact pack persistence and reproduction, and these impacts are likely to be greatest when pack sizes are small (< 6) and harvest overlaps the breeding season.

The role of individual breeders in maintaining pack cohesion appears moderated by the availability of replacement breeders as indicated by the effect of pack size. Consistent with the findings of Brainerd et al (2008), our analysis indicates that large packs are more likely to persist following breeder mortality than small packs (Fig. 2.2). Large packs are more likely to have multiple breeders, unrelated adoptees or reproductively viable related individuals present as replacement breeders (Meier et al. 1995; Mech & Boitani 2003), whereas small packs are more likely to have young of only the previous year (Mech 1999). Heterogeneity in the reproductive value of individuals in social groups may therefore depend on group size, such that the reproductive value of a single breeder in a small group is higher than the reproductive value of individual breeders in large groups.

The availability of replacement breeders may increase with the overall size of the population as well as pack size. Brainerd et al. (2008) found that breeder replacement in wolf packs occurred more quickly in saturated versus recolonizing populations. Thus the effects of breeder loss on pack fate could be moderated by the availability of replacement breeders not only within the pack, but in the population and surrounding areas. The wolf population in DNPP is generally considered to be a saturated population at or near carrying capacity (Mech et al. 1998), and therefore our results may represent the minimum impacts that breeder loss can have on pack and population dynamics.

We found that packs that lost both breeders were more likely to dissolve, as did Brainerd et al (2008). However, loss of both breeders confounded the influence of sex of breeder loss with the numeric impacts of the loss of two individuals. The influence of female versus male loss was more explicit, and as expected, mortality of a female breeder destabilized packs more often than the loss of a male breeder. Female parturition and the care of neonates and young pups are essential to pack reproduction and recruitment. Thus mortality of female breeders, especially when timed during the breeding season, has disproportional impacts on pack fate and may represent a loss of the reproductive capacity for the entire pack for that year.

Overall, most packs maintained cohesion and reproduced despite breeder loss, indicating a high degree of resilience and rapid replacement of breeders. These high reproductive rates imply that either successful replacement of the lost breeder occurred prior to the breeding season, or that multiple breeders were present in the pack which mitigated the loss of one breeder. Interestingly, intact wolf packs in the eastern region of DNPP exhibited high den site fidelity, regardless of whether a pack experienced lost breeders or not. Den site fidelity may thus be related to pack persistence or other factors rather than breeder continuity. However, reproductive success was substantially reduced for packs that experienced breeder loss and remained intact. This result supports findings from other species that found reductions in reproductive capacity following disruption of the social group. For example, female African elephants (*Loxodonta africana*) from disrupted groups had a significantly lower reproductive output than females from intact social groups (Gobush et al. 2008).

Although not explicitly considered in our analysis, additional sources of heterogeneity in individual breeders such as body mass, age or even coat colour may also affect reproductive success (Mech 1995; Stahler et al. 2013). Breeder age and experience may be particularly important, because younger individuals and those breeding for the first time have lower reproductive success (Anderson 1986; Stacey & Koening 1990; Mech et al. 1998; Heinze & Schrempf 2012). Thus, even if lost breeders are replaced by subordinates, recruitment success could be reduced. If replacement breeders tend to be younger than breeders that died, age effects may reduce the ability of populations to compensate for breeder losses.

Pack dissolution rates appeared to have weak negative effects on population growth of wolves in DNPP. However, population growth rates following years of high breeder loss and pack dissolution did not remain low, indicating that strong compensatory mechanisms buffered against longer-term population level impacts. Because our regression analyses did not account for sampling and measurement variance in the population estimates, results should be interpreted with caution.

Annual rates of human-caused mortality in DNPP wolves ranged from 3-7% during 1986-2002 (Adams et al. 2008), well below the level expected to reduce rates of population growth (reviewed in Fuller *et al.* 2003, Adams *et al.* 2008). Despite these low harvest rates, we found that anthropogenic mortality of breeders increased the probability of pack dissolution. Harvest may be a largely additive source of mortality for wolves rather than a compensatory one (Adams et al. 2008; Murray et al. 2010; Sparkman et al. 2011), especially in small, isolated or recolonizing populations. The influence of breeder loss in small, isolated or recolonizing populations may be greater than reported in our study of a saturated wolf population, because the time for breeder replacement and subsequent reproduction is increased in those populations (Brainerd et al. 2008). Therefore, the loss of breeders in regions with higher harvest rates or in low density or unsaturated populations may have lasting negative effects on population growth.

Our study is the first to explicitly link the effects of breeder loss to population growth rates in wolves, and further research on these relationships is needed to quantify the importance of breeders within low density or unsaturated populations. With grey wolf recovery and delisting from the Endangered Species Act, wolf management plans in several states (Idaho, Michigan, Minnesota, Montana, Wisconsin and Wyoming) include public harvest seasons that overlap with the wolf breeding season. For regions with recovering wolf populations, and those with small average pack sizes, harvest that occurs during the breeding season could have disproportionate impacts on pack fate and population growth, indicating that wolf recolonization into new areas could be slower than expected. The implications of these findings extend to other socially structured species with reproductive suppression of subordinates and to species where harvest coincides with breeding season. In such cases, we may expect impacts on social structure and population growth beyond those anticipated by population models that ignore the role of reproductive individuals.

2.6 Acknowledgements

This paper is dedicated to the memory of Thomas J. Meier, who successfully led the wolf monitoring program in DNPP from 2004 until 2013 and provided invaluable mentorship and guidance to this study. Funding was provided by the National Park Service and the US Geological Survey. The Alaska Department of Fish and Game provided valuable assistance and cooperation. L. D. Mech, L. Adams, J. Burch, B. Dale and T. Meier pioneered the long term study and collected data from 1986 to 2012. J. Blake, C. Rosa and K. Beckmen conducted necropsies. L. Adams, S. Arthur, J. Falke, G. Hilderbrand, M. Lindberg, and K. Sivy, and K. Titus provided valuable comments on earlier versions of this manuscript. Work was conducted under annual National Park Service permits and Institutional Animal Care and Use protocol approval (NPS IACUC 2010-1), annual State of Alaska Department of Fish and Game scientific permits, and the University of Alaska permit (253217-3).

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2.8 Figures

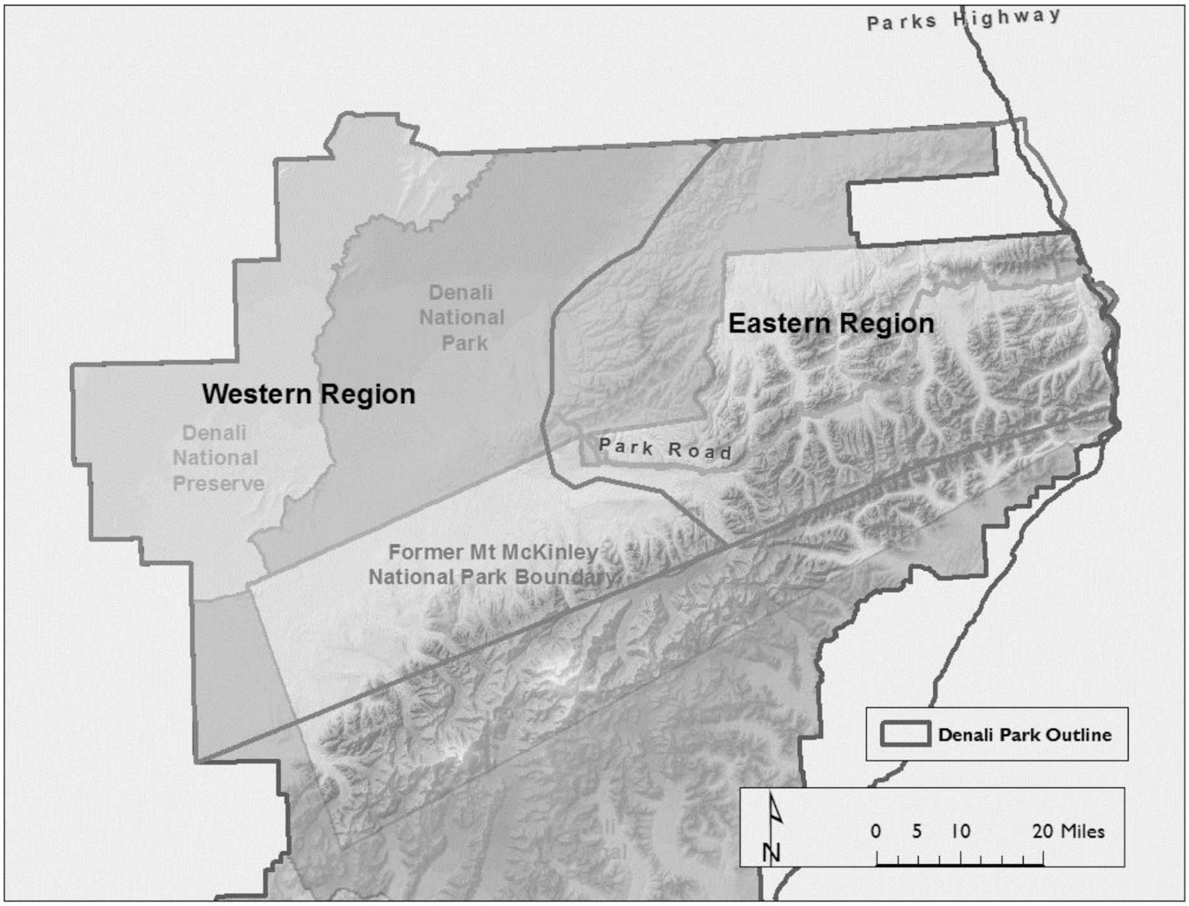

Figure 2.1. Map of study area and geographical sub population regions for long term monitoring of grey wolf packs in Denali National Park and Preserve, Alaska, USA.

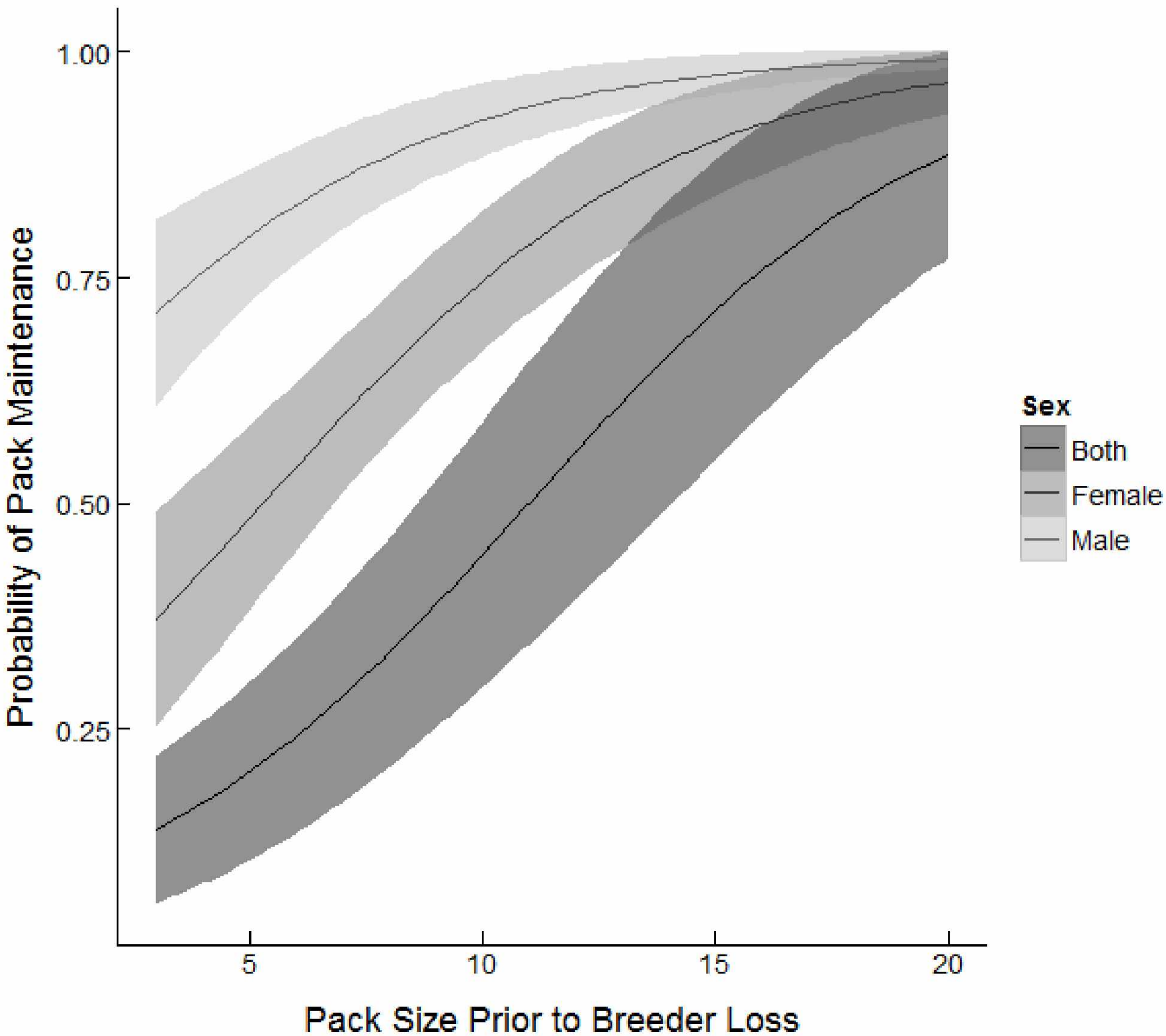

Figure 2.2. Effect of pack size prior to breeder loss and sex of breeder(s) lost on the probability of grey wolf packs remaining intact in Denali National Park, Alaska, USA, 1986-2012. Shaded areas show 95% confidence intervals around predicted probabilities.

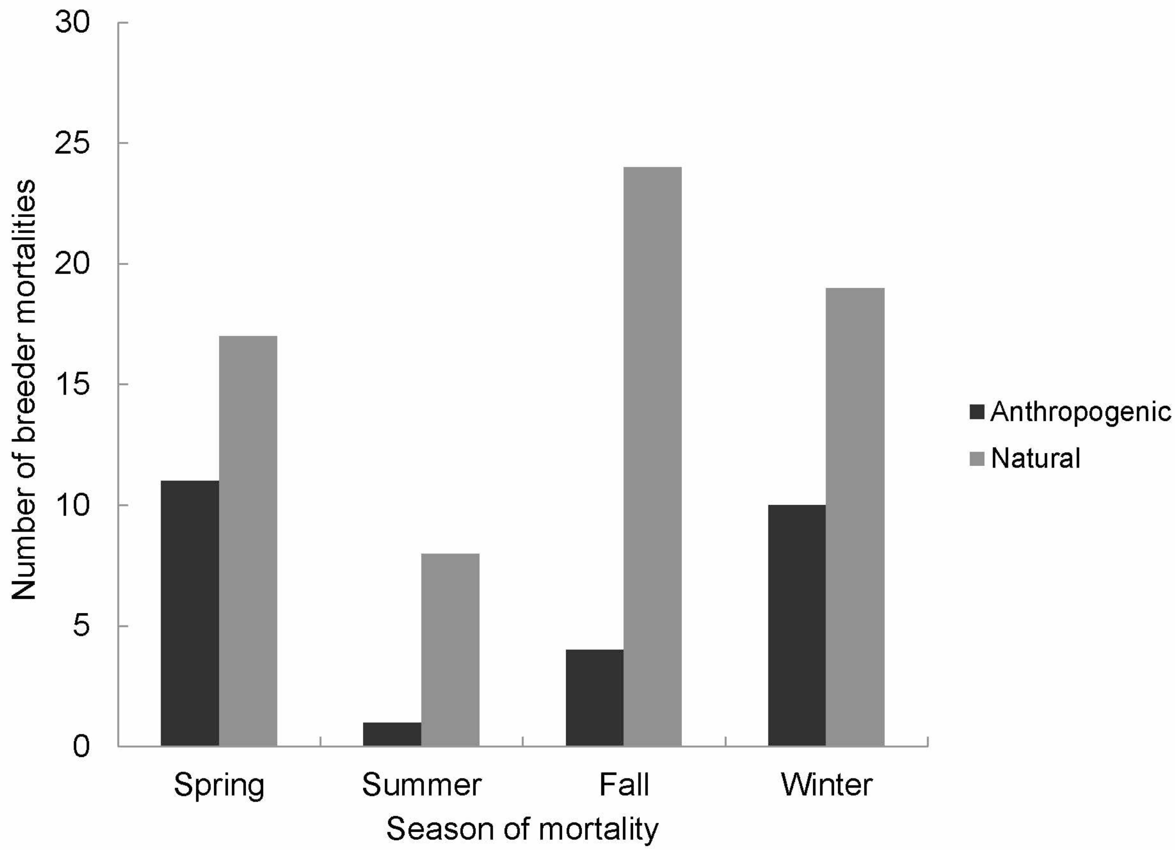

Figure 2.3. Total number of mortalities of breeding grey wolves by season and type of mortality in Denali National Park, Alaska, USA, 1986-2012 (n = 94). Spring = February-April, Summer = May-July, Fall = August-October, Winter = November-January. Anthropogenic mortality includes hunting, trapping, and capture-related deaths; natural mortality includes intraspecific strife, starvation, injuries and accidents.

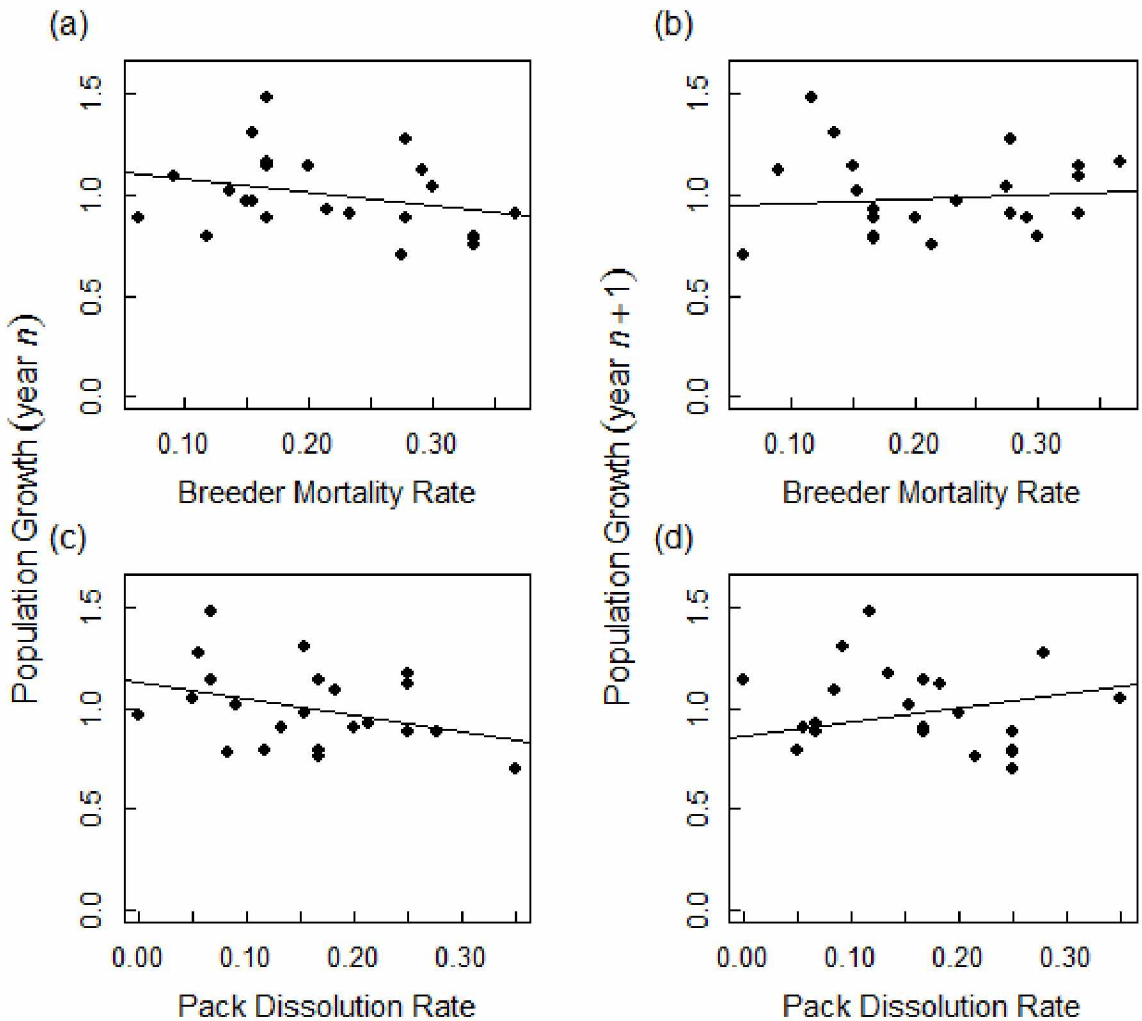

Figure 2.4. Effect of breeder mortality and pack dissolution on annual population growth of grey wolves in Denali National Park, Alaska, USA, 1986-2012 with and without a time lag. Effect of breeder mortality rate in year n on population growth rate in (a) year n and (b) year n+1. Effect of pack dissolution rate in year n on population growth rate in (c) year n and (d) year n+1. Non-significant regression lines are displayed.

2.9 Tables

Table 2.1. Cases of grey wolf pack persistence and dissolution following breeder mortality in Denali National Park, Alaska, USA, 1986-2012.

Breeder Mortality	Pack Persist	Pack Dissolve
Both	5	11
Female	27	14
Male	31	6
All Breeder Mortality	63	31

Table 2.2. Candidate model set and model selection criteria evaluating factors potentially affecting grey wolf pack maintenance following breeder mortality in Denali National Park, Alaska, USA, 1986-2012. M-Z Pseudo-R^2 estimates the amount of deviance in the data explained by each model.

Model	# Parameters	AICc	ΔAICc	Model Likelihood	AICc Weight	M-Z Pseudo-R^2
PP[2]+Sex[3]	4	103.44	0.00	1.00	0.49	0.33
PP+Sex+Mort[4]	5	104.84	1.40	0.50	0.24	0.34
PP+Season[5]+Sex	7	105.41	1.97	0.37	0.18	0.39
PP+Season+Sex+Mort[6]	8	107.64	4.20	0.12	0.06	0.39
Sex	3	111.59	8.14	0.02	0.01	0.18
Season+Sex	6	113.60	10.16	0.01	0.00	0.25
Sex+Mort	4	113.61	10.17	0.01	0.00	0.18
PP+Season	5	114.74	11.30	0.00	0.00	0.25
PP	2	115.44	12.00	0.00	0.00	0.13
Season+Sex+Mort	7	115.93	12.49	0.00	0.00	0.25
PP+Season+Mort	6	117.02	13.58	0.00	0.00	0.25
PP+Mort	3	117.22	13.78	0.00	0.00	0.14
Season	4	121.43	17.99	0.00	0.00	0.09
Mort	2	123.29	19.85	0.00	0.00	0.00
Season+Mort	5	123.48	20.04	0.00	0.00	0.10

[2] Pack size prior to breeder loss
[3] Sex of breeder loss
[4] Cause of mortality: natural or anthropogenic
[5] Season of breeder loss: spring, summer, fall or winter
[6] Global Model

Table 2.3. Parameter estimates for factors included in the top-ranked models (ΔAIC < 2) predicting the probability of pack maintenance following breeder mortality in Denali National Park, Alaska, USA, 1986-2012. See Table 2.2 for all models. PackPrior is the pack size prior to breeder loss.

Parameter	β (Model Averaged)	SE	95% CL		Odds ratio (Model Averaged)
			Lower	Upper	
(Intercept)	-2.42	1.07	-4.52	-0.33	0.09
PackPrior	0.24	0.08	0.07	0.4	1.27
Sex (F)[7]	1.22	0.71	-0.17	2.61	3.39
Sex (M)[a]	2.7	0.77	1.19	4.22	14.88
Cause Mortality (Natural)[8]	0.48	0.62	-0.73	1.69	1.62
Season (Spring)[9]	-1.12	0.73	-2.54	0.31	0.33
Season (Summer)[c]	0.18	1.00	-1.79	2.14	1.20
Season (Winter)[c]	-1.16	0.71	-2.56	0.24	0.31

[7] β and odds ratio estimates relative to mortality of both breeders
[8] β and odds ratio estimates relative to anthropogenic cause of mortality
[9] β and odds ratio estimates relative to mortalities that occur in fall

Table 2.4. Cases of pack denning (reproduction), successful recruitment and den site fidelity in relation to breeder mortality for grey wolf packs in Denali National Park, Alaska, USA, 1997-2012.

Breeder Mortality	Denning	No Denning	Recruitment	No Recruitment	Den Fidelity[10]	New Den	No Denning
Both sexes	2	3	2	0	2	0	4[11]
Female	10	0	6	4	4	1	0
Male	8	2	6	2	4	1	2
Total							
Breeder Mortality	20	5	14	6	10	2	6
No Breeder Mortality	52	2	49	3	20	16	1

[10] Den fidelity data is a subset of denning data for which we have information on denning in the prior year
[11] Includes 2 cases of pack dissolution following breeder mortality

2.10 Supporting Information

Table S2.1. Pack life spans for gray wolf packs monitored in Denali National Park, Alaska, USA, 1986-2012.

Pack Name	Formed	Ended	Pack Fate	Pack Life Span	End Preceded By Breeder Loss
100 Mile	1996	2004	End	8	Female
Alma Lakes	≤1986	1986	End	≥1	Unknown
Bearpaw1	≤1987	1988	End	≥1	Unknown
Bearpaw	2004		Continue	8	NA
Beaver Fork	1995	1999	End	4	Both
Birch Creek	≤1987	1991	End	5	Unknown
Birch Creek N	1991	1992	End	1	Female
Birch Hills	1998	2000	End	2	Male
Boot Lake	2007	2009	Censored	≥2	NA
Brooker	2001	2003	End	2	Male
Caribou Creek	1996	1998	End	2	Female
Castle Rocks	1988	1988	End	<1	Both
Castle Rocks2	2003	2005	End	2	Both
Castle Rocks3	2006	2008	End	2	Female
Chilchukabena	1990	1992	End	2	Female
Chitsia	2004	2008	End	4	Both
Chitsia Mountain	1988	1994	End	6	Female
Clearwater	≤1986	1990	End	≥4	Male
Corner Lake	1994	1998	End	4	Female
Death Valley	2000	2003	End	3	Both
East Fork	1986		Continue	26	NA
Ewe Creek	1987	1989	Censored	≥2	NA
Foraker	1989	2001	End	12	Both
Glen Creek	2000	2000	End	<1	Both
Grant Creek	2001		Continue	11	NA
Hauke Creek	2006	2008	End	2	Male
Headquarters	≤1986	1995	End	≥9	Female
Herron	2001	2006	End	5	Unknown
Highpower	1988	1992	Censored	≥4	NA
Hot Slough	2007		Continue	5	NA
Iron Creek	2009		Continue	3	NA
Jenny Creek	1993	1994	End	<1	Unknown
Kantishna River	2000	2006	End*	6	Both
Little Bear	1988	1995	End	7	Both
McKinley River1	1987	1996	End	9	Male
McKinley River	2004	2008	End	4	Female

Pack Name	Formed	Ended	Pack Fate	Pack Life Span	End Preceded By Breeder Loss
McKinley Slough	1999		Continue	13	NA
McLeod	1987	1997	End	10	Female
McLeod West	1991	1992	Censored	1	NA
McLeod2	2007	2008	End	1	Both
Moose Creek	2009	2010	End	1	Female
Mt Margaret	2000	2009	End	9	Both
Muddy River	2000	2004	End	4	Female
Nenana River	2009		Continue	3	NA
North Fork	1998	2002	End	4	Both
Otter Creek	1998	2002	End	4	Unknown
Otter Lake	2009	2010	End	1	Both
Pinto	2005	2008	End	3	Unknown
Pinto Creek	1997	2003	End	6	Female
Pirate Creek	1987	1988	End	<1	Female
Sanctuary	1995	2001	End	6	Both
Sandless Lake	1997	1998	End	1	Unknown
Savage1	1992	1995	End	4	Female
Savage	2007	2008	End	1	Unknown
Slippery Creek	1991	1992	End	2	Male
Somber	2006		Continue	6	NA
Stampede	1988	2001	End	13	Female
Starr Lake	2000		Continue	12	NA
Stony	1995	1999	End	4	Female
Straightaway	1999	2006	End	7	Male
Sushana	≤1986	1986	End	<1	Unknown
Swift Fork	1988	1989	End	1	Unknown
Thorofare	1992	1993	End	2	Unknown
Toklat Springs	2004	2012	Censored	≥8	NA
Tonzona	2007	2009	End	2	Both
Totek Hills	2007	2009	Censored	≥2	NA
Turtle Hill1	1992	1995	End	3	Female

Chapter 3

Implications of harvest on the boundaries of protected areas for wolf viewing opportunities[1]

3.1 Abstract

The desire to see free ranging large carnivores in their natural habitat is a driver of tourism in protected areas around the globe. However, large carnivores are wide-ranging and subject to human-caused mortality outside protected area boundaries. The impact of harvest (trapping or hunting) on wildlife viewing opportunities has been the subject of intense debate and speculation, but quantitative analyses have been lacking. We examined the effect of legal harvest of wolves (Canis lupus) along the boundaries of two North American National Parks, Denali (DNPP) and Yellowstone (YNP), on wolf viewing opportunities within the parks during peak tourist season. We used data on wolf sightings, pack sizes, den site locations, and harvest adjacent to DNPP from 1997-2013 and YNP from 2008-2013 to evaluate the relationship between harvest and wolf viewing opportunities. Although sightings were largely driven by wolf population size and proximity of den sites to roads, sightings in both parks were significantly reduced by harvest. Sightings in YNP decreased by 31% following years with harvest of a wolf from a pack and sightings in DNPP decreased by 57% during the absence of a harvest buffer zone relative to years with the buffer. These findings show that harvest of wolves adjacent to protected areas can reduce sightings within those areas despite minimal impacts on the size of protected wolf populations. Consumptive use of carnivores in these areas may therefore reduce

[1]Prepared for submission to Conservation Biology as Borg. BL, SM Arthur, NA Bromen, KA Cassidy, R McIntyre, DW Smith, and LR Prugh 2015. Implications of harvest on the boundaries of protected areas for wolf viewing opportunities.

their potential for non-consumptive use, and these tradeoffs should be considered when developing regional wildlife management policies.

3.2 Introduction

Large carnivore conservation relies heavily on sustaining populations within protected areas (Brashares et al. 2001), and protection within these regions provides the majority of viewing opportunities for these species (Walpole & Thouless 2005). The desire to see iconic, free ranging large carnivores is a driver for wildlife tourism around the globe and may improve acceptability of their presence by the general public and contribute to conservation goals (Frank et al. 2005; but see Dickman et al. 2011). However, large predators are wide-ranging and seldom confined within the boundaries of protected areas, creating difficult transboundary management issues. Outside and even inside of protected areas, conflict with humans is the single most important cause of mortality for large carnivores (Woodroffe & Ginsberg 1998; Murray et al. 2010). Yet the link between human-caused mortality of carnivores adjacent to protected areas and viewing opportunities within a protected region has not been evaluated quantitatively.

In North America, gray wolves (*Canis lupus*) are emblematic of management issues occurring at the borders of protected areas. Protection of wolves in Yellowstone National Park (YNP) and Denali National Park and Preserve (DNPP) provides the opportunity for thousands of visitors to see wolves each year, but these wide-ranging carnivores often travel across park boundaries onto other public or private lands. Mortality of individual wolves from frequently viewed packs due to hunting or trapping outside these parks has sparked widespread controversy and prompted concern regarding the impact of these losses on population and pack dynamics. Although harvest (hunting or trapping) occurring outside park boundaries may not have population-level effects, harvest of particular individuals can lead to the decline or dissolution of entire packs (Thurber et al. 1994; Borg et al. 2015). If the packs or individuals most susceptible to harvest are those that provide the majority of viewing opportunities to visitors of protected areas, then harvest may influence wolf sightings even if harvest levels are too low to reduce population size.

National Park Service mandates include providing opportunities for visitor enjoyment, of which wildlife viewing is an important component in DNPP and YNP. Viewing large carnivores, particularly wolves and grizzly bears (*Ursus arctos*), is cited by visitors as one of the main reasons they come to YNP (Duffield et al. 2008) and is a main indicator of a satisfying visitor experience in DNPP (Manning & Hallo 2010). Additionally, in Alaska where wolves are among the most desired species for viewing (Shea & Tankersley 1991), state wildlife management includes mandates to provide for multiple uses, including non-consumptive uses such as wildlife viewing (Alaska Department of Fish and Game 2006). In Montana, wildlife watching is listed by visitors and state residents as one of the primary activities in the state (U. S. Department of the Interior et al. 2011). Wildlife viewing also brings an important socio-economic benefit to the states. Wolf watching activities in YNP following the reintroduction of wolves in 1995 brings an estimated $35 million annually to the states of Idaho, Montana and Wyoming (Duffield et al. 2008), and wildlife viewing is a driver of tourism for DNPP as well as for the state of Alaska (Stynes & Ackerman 2010; U. S. Department of the Interior et al. 2011). At the same time, states are also mandated to provide for consumptive uses of wildlife, and harvest of wolves can provide significant economic benefits as well (National Research Council 1997).

As part of the delisting process for gray wolves in Montana, Wyoming and Idaho, each state has developed wolf management plans that include wolf hunting seasons (for details on state management: www.westerngraywolf.fws.gov), prompting concern that hunting may impact wolf viewing opportunities in YNP (Schweber 2012). In DNPP, a buffer zone prohibiting the trapping and hunting of wolves was established in key regions bordering DNPP from 2000 to 2010 (Fig. 3.1). The buffer was abolished in March 2010 and viewing rates in DNPP subsequently declined (Borg 2014), raising concerns that harvest of wolves near park boundaries might have been responsible.

The main objective of this study was to assess effects of wolf harvest on visitor sightings of wolves in YNP and DNPP. We first examined levels of wolf harvest adjacent to each park and the composition of harvested wolves to determine whether breeding and collared wolves were more or less susceptible to harvest. Concurrent analyses showed that breeding wolves were more likely to be near the Denali Park Road than non-breeding wolves (Borg et al., unpublished), indicating that breeding wolves may contribute disproportionately to sightings. However, we anticipated that less experienced (younger, non-breeding) wolves would be more likely to be harvested than the generally more experienced breeding wolves (Adams et al. 2008 but see Peterson et al. 1984; Ballard et al. 1987). If this was the case, we expected that harvested wolves may be relatively unimportant to sightings, thereby reducing the potential effect of harvest on viewing opportunities. However, in YNP, the presence of radio-collars on wolves, regardless of breeding status, may increase sighting opportunities for visitors because NPS staff routinely scans for signals from collared animals to assist in locating and viewing wolves. Therefore, if there was disproportional harvest of collared wolves (regardless of breeding status), harvest could decrease viewing opportunities, especially in YNP.

We analyzed data on wolf sightings, pack sizes, den site locations, and harvest adjacent to DNPP from 1997-2013 and YNP from 2008-2013 to evaluate the relationship between harvest of wolves and wolf viewing opportunities. We hypothesized that the presence of harvest (or absence of the harvest buffer) would reduce wolf sightings. Alternatively, changes in wolf population size and den site proximity to park roads could be the main drivers of wolf sightings, and harvest could have comparably negligible effects.

3.3 Methods

3.3.1 Study areas

The DNPP study area encompassed 6,350 km^2 of the eastern region of the park and adjacent areas north of the Alaska Range (Fig. 1.1). Elevation ranges from 150-3,000 m and contains habitat patches of boreal forest, high alpine, braided rivers, and willow-lined creeks. The diversity of habitat types supports populations of caribou (*Rangifer tarandus*), Dall's sheep (*Ovis dalli*), and moose (*Alces alces*) which constitute the main prey base for wolves in the region. The YNP study area encompassed approximately 1,000 km^2 of the Northern Range within and adjacent to the park (Fig.3.2). Elevation ranges from 1,500–2,400 m, with lower elevations characterized by large open meadows and shrub steppe vegetation and higher elevations characterized by coniferous forests (Houston 1982). Elk (*Cervus elaphus*) are the main prey for wolves in this region, but wolves also prey secondarily on bighorn sheep (*Ovis canadensis*), bison (*Bison bison*), moose, mountain goat (*Oreamnos americanus*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*) and white-tailed deer (*Odocoileus virginianus*).

3.3.1 Data collection

3.3.1.1 Population and pack counts

Biologists have radio-collared wolves in the DNPP study region since 1986 (Mech et al. 1998) and within YNP since the reintroduction of wolves in 1995 (Bangs & Fritts 1996). Each year, 6–22 wolves from 10–20 packs were fitted with radio collars in DNPP (Borg & Burch 2014) and 10–20 wolves from 5–12 packs were collared in YNP (Smith et al. 2012, see Sikes et al. 2011 for handling protocols). Wolf project staff in both YNP and DNPP used a combination of aerial and ground monitoring techniques to collect data on wolf locations, numbers of pack members, pack composition, active den site locations and use, breeding status of individual wolves and timing and suspected causes of mortality (Mech et al. 1998; Smith & Bangs 2009).

3.3.1.2 Harvest

All areas outside the DNPP boundary were open to hunting and trapping under state regulation, with the exception of a closed area established by the Alaska Board of Game in 2000, expanded in 2001 and 2002 (Fig. 3.1), and abolished in 2010. Although the closed area was relatively small (75 km^2 in 2000, 233 km^2 from 2002-2010), it included areas that supported high seasonal densities of caribou and associated wolf activity (Mech et al. 1998). In Game Management Units (GMU) 20A and 20C adjacent to the park’s boundaries, the hunting season ranged from mid-August to the end of April or May with a bag limit ranging from 5-10 wolves, and the trapping season spanned November 1– April 30 with no bag limits for either unit. Subsistence and sport hunting and trapping were permitted in the Preserve and new park additions of DNPP, but all harvest was prohibited in the area of the original Mt. McKinley National Park (Fig. 3.1). Outside YNP, wolves were hunted in 2009, 2011 and 2012 in Idaho and Montana, and in 2012 in Wyoming, with open seasons and limits that varied among hunting units within states. Wolves were not harvested in 2010 due to relisting under the Endangered Species Act. The numbers of wolves harvested from regions adjacent to park boundaries were obtained from state harvest records and mortality of collared wolves.

3.3.1.3 Harvest of collared and breeding wolves

To examine whether collared and breeding wolves were harvested disproportionately, we used chi-squared and Fisher exact tests to compare the proportion of collared and breeding wolves harvested in areas surrounding each park with their proportions in each park population. In DNPP, we used mortality records to determine the number of collared wolves that were shot or trapped in Uniform Coding Units (UCU) adjacent to DNPP (UCUs 605, 607, and 502) from 1996 to 2012 (Fig 3.1). We included all recorded wolf harvest within UCUs 605 and 607 in analyses because these UCUs were within the buffer zone or immediately adjacent to DNPP (Fig. 3.1). UCU 502 extended north beyond DNPP and we therefore attempted to include only instances of wolves harvested in UCU 502 that occurred within the former buffer zone using information on the location of harvest. Instances of harvest with unknown locations within UCU 502 were included in the count of harvested wolves in the region. In YNP, we consulted with state agencies to estimate the number of collared and/or breeding wolves and the total number of wolves harvested outside of YNP that were from packs that lived predominantly in YNP.

Harvested wolves that were uncollared were judged to have originated from YNP packs if the ages, colors, and sexes matched wolves recently missing from YNP.

We pooled data across years with wolf harvest (1996-2012 for DNPP and 2009, 2011, and 2012 for YNP). We calculated the proportion of collared wolves in the population as the number of individuals collared in or before year *t* that were still alive by August of year *t* divided by the fall population estimate. Similarly, we determined the proportion of breeders in the population as the number of collared individuals identified as breeders divided by the fall population estimate. We restricted our analysis to collared breeders because identification of uncollared breeders in the harvest was not always possible. We determined the proportion of collared or breeding wolves in the harvest as the number of collared/breeding wolves harvested divided by the number of wolves harvested in surrounding UCUs (DNPP) or from YNP packs.

3.3.2.4 Sighting data

Each study area is bisected by a road (Denali Park Road in DNPP and Northeast Entrance Road in YNP, Figs 3.1,3.2) providing visitor access to the region and wolf viewing opportunities.

DNPP

We used data on wildlife sightings along the Denali Park Road collected during bus trips into the park from the Savage River entrance station at mile 15 to Eielson Visitor Center at mile 66 from 1997-2013. Data were collected by bus drivers as written observations or on panels installed on buses and by park staff as written observations or on handheld devices. Observers recorded all sightings of wolves during all westbound trips (see Supporting Information for more details).

YNP

From 2008 to 2013, YNP staff (R. McIntyre) traveled through the Lamar Canyon and Little America region (Fig. 3.2) every morning (from approximately 0430 or 0500 to 1100 or 1200 hours) and consistently recorded all direct sightings of wolves. These six years represent a sample of years with and without harvest, consistent monitoring of sightings, and a relatively stable wolf population. We reviewed the daily field notes and recorded the start and end time of each daily observation period and attributes of every wolf sighting (location and duration of sighting, number of wolves seen, pack affiliations) in June, July and August.

3.3.3 Annual probability of sightings metric

We calculated the annual probability of sighting metric in DNPP as the proportion of bus trips where at least one wolf was seen. In YNP, we calculated this metric as the number of days with direct sightings of wolves in Lamar Valley or Little America (Fig. 3.2) divided by the number of days in the observation period (i.e. number of days in June, July and August), corrected for effort:

$$YNP\ P_{sighting} = \frac{S_t}{O_t} \times \frac{E_t}{E_{max}}$$

where S_t is the number of days with sightings in year *t*, O_t is the number of days in the observation period, E_t is the hours of effort in year *t*, and E_{max} is the maximum number of hours in the field from sampled years.

We predicted that the annual probability of sighting for a wolf was positively related to wolf population size and den site proximity to the roads and negatively related to the number of wolves or breeders harvested. We examined 2 metrics of population size: spring estimates of total wolf population size in each study area (TotalPop), and a metric that combined the estimated size of packs whose home range overlapped park roads (road packs) with distances from den sites to the nearest road (the Pack Near Road Index, or PNRI). TotalPop represented a simple and potentially useful metric that could be calculated in spring prior to denning while PNRI was a metric that combined a spatially-explicit measure (den site distance from the road) with a population measure (road pack size). We initially investigated a separate covariate for road pack size alone (Supporting Information) and found that the metric that combined road pack size and den distance (PNRI) explained more variance in sightings. We therefore used PNRI in our final model set.

TotalPop was obtained by compiling spring wolf pack counts for packs in each study area. We used ArcGIS 10.0 (Environmental Systems Research Institute, Redlands, CA) to assess home range overlap with park roads. PNRI was calculated using the "near" tool in ArcGIS 10.0 to determine the distance of den sites from the nearest location on the road. For all road packs in the sighting year, we divided the pack size by the distance of the pack's den or rendezvous site to the road (in cases where there was more than one den or rendezvous site used, we used the mean of the distances of multiple den or rendezvous sites) and defined the PNRI as the sum of these measures for all packs in the sighting year.

For DNPP, we evaluated three metrics describing wolf harvest: number of wolves harvested in the region (WolfHarv), harvest of breeding wolves (BreedHarv) and the presence/absence of a wolf trapping buffer (Buffer) located outside of DNPP (Fig. 3.1).WolfHarv was the number of wolves harvested in Uniform Coding Units (UCUs) 605 and 607 (Fig. 3.1) in the regulatory year prior to the sighting year (July 1 of year t-1 to June 30 of year t). BreedHarv was a binary factor describing if a breeding wolf from a road pack was harvested prior to the sighting year. The trapping buffer was present from 2000-2010 and absent 1997-1999 and 2011-2013. In YNP, we obtained information on the number of wolves harvested outside of YNP from Yellowstone Wolf Project staff in collaboration with state wildlife agency professionals in Montana, Wyoming, and Idaho.

3.3.4 Effect of harvest on sightings

We evaluated factors that influenced annual wolf sightings in DNPP using a suite of generalized linear models and Akaike information criterion corrected for sample sizes (AICc) to rank models (Burnham & Anderson 2002). We used the glm function in Program R (R Core Team 2014) to model wolf sightings using a binomial distribution with the response variable as the annual probability of wolf sightings, weighted by the number of trips per year to account for sample size. Predictor variables consisted of the two population and three harvest metrics described above, and our model set consisted of 14 models selected a-priori that included 1-3 predictors per model (Table 3.1). We used the MuMIn package in R (Barton 2014) for model selection and derived parameter estimates and associated standard errors from the top ranked model. We calculated the amount of deviance explained by each model (pseudo-R^2), which is analogous to R^2 of linear regression (Hagle & Mitchell 1992):

$$PseudoR^2 = \frac{model\ deviance - null\ deviance}{null\ deviance}$$

We investigated how accounting for an estimate of overdispersion influenced model selection and parameter estimate uncertainty. We compared estimates of population size, PNRI, and annual probability of sightings in years with and without the buffer zone using a one-tailed t-test.

We lacked sufficient years of data in YNP to construct quantitative models of sightings including all covariates. Therefore, we visually examined patterns in the annual sighting metric in relation to TotalPop and PNRI. We compared annual probability of sightings in years with and without harvest of wolves from packs in the prior regulatory year using a one-tailed t-test.

3.4 Results

3.4.1 Harvest of collared and breeding wolves

3.4.1.1 DNPP

Wolves were harvested on state land adjacent to DNPP in 16 of the 17 years in our dataset (1996– 2012). Across all 17 years, on average 5 (SD 3.5) wolves were harvested each year (Supporting Information). Pooled across all years with harvest, neither the proportion of collared wolves in the harvest (0.25) nor the proportion of known (collared) breeding wolves in the harvest (0.16) were significantly different than expected given their frequency in the population (collared wolves in population: 0.29, $\chi 2 = 0.610$, df = 1, $P = 0.44$, collared breeders in population: 0.17, $\chi 2 = 0.072$ df = 1, $P = 0.79$).

3.4.1.2 YNP

In 2009, 4 park wolves were harvested from the study area. In 2011, 2 wolves ranging primarily within YNP but not considered members of a road pack were shot close to the park boundary. In 2012, 9 wolves that primarily lived within the Northern Range study area were harvested and a total 12 wolves that lived in the entire YNP were harvested. The proportion of collared wolves in the harvest (0.53) was greater than expected given the proportion of collared wolves in the

Northern Range population (0.24, Fisher's exact test: $P = 0.03$). Similarly, in the entire YNP region, the proportion of collared wolves in the harvest (0.56) was greater than expected given the proportion of collared wolves in the YNP population (0.26, Fisher's exact test: $P = 0.01$, Supporting Information). The proportion of collared breeding wolves in the harvest (0.21) was not significantly different than the proportion of collared breeders in the Northern Range (0.17, two-sided fisher's exact test, $P = 0.37$).

3.4.2 Annual Probability of Sighting

3.4.2.1 DNPP

Both the number of wolves denning near the road and wolf harvest influenced the mean probability of viewing wolves in DNPP. The top ranked model included the Pack Near Road Index (PNRI), the presence of the wolf harvest buffer, and the number of wolves harvested (Table 3.1). The number of wolves denning near the road was positively associated with the probability of viewing wolves (PNRI: $\beta = 24.6 \pm 3.13$ SE). The presence of the buffer was also positively associated with the probability of viewing wolves (Buffer presence: $\beta = 1.0 \pm 0.17$), whereas the number of wolves harvested in the prior year was negatively associated with the probability of viewing a wolf (WolfHarv: $\beta = -0.1 \pm 0.02$, Table 3.2). Accounting for an estimate of overdispersion increased model selection uncertainty and inflated estimates of variance but did not alter the ranking of top models nor change our inference based on parameter estimates (with the exception of widening the confidence interval for WolfHarv to slightly overlap zero, Supporting Information).

The annual probability of sighting appeared to roughly follow the trend of the annual PNRI and spring population size, with peaks in sightings coinciding with peaks in either PNRI or total population size (Fig. 3.3, see Supporting Information for figure with road pack size). Population size, PNRI and the probability of sighting were significantly higher in years when the buffer zone was in place (Table 3.3, Fig. 3.5).

3.4.2.2 YNP

There were two years of sighting data following harvest from YNP road packs (2010 and 2013) and four years with no prior road pack harvest (2008, 2009, 2011 and 2012). The annual probability of sighting metric for YNP appeared to roughly mirror spring population size and PNRI, but sightings were lower in years following harvest of wolves from road packs than in years with similar population size (Fig. 3.4, see Supporting Information for figure with road pack size). The mean probability of sighting was significantly lower following years with harvest of road pack wolves (0.54 ± 0.127 SE) than in years without harvest of a road pack wolf (0.78 ± 0.084 SE, $t_4 = 2.88$, $P = 0.02$, Fig. 3.5). Including 2012 as a post-harvest year, the mean probability of sighting was not significantly different between years following harvest (0.64 ± 0.040 SE) and years without harvest (0.76 ± 0.086 SE, $t_4 = 0.92$, $P = 0.21$).

3.5 Discussion

This study provides the first quantitative evidence that harvest of wildlife adjacent to protected areas can reduce wildlife sighting opportunities. Harvest of wolves near park boundaries substantially reduced sightings in both Denali and Yellowstone National Parks. The probability of viewing a wolf was 45% greater in YNP following years with no harvest of a wolf from a road pack, and sightings in DNPP were more than twice as high in years with the presence of a wolf harvest buffer (Fig 3.5). Sightings decreased as the number of wolves harvested adjacent to DNPP increased, although the relationship was relatively weak. These findings imply a trade-off between harvest (i.e., consumptive use) of wolves and the non-consumptive viewing opportunities and associated economic benefits. Additionally, we found that population size, pack size and den site location were strong drivers of sighting opportunities for wolves within these protected areas. These findings suggest that harvest should have particularly strong effects on sightings when harvest reduces population size or affects breeding behavior within protected regions.

Although harvest of wolves in our study systems may not have occurred at rates generally considered sufficient to reduce population size (reviewed in Fuller et al. 2003), harvest may influence sightings through other mechanisms. Behavioral avoidance of humans by wolves following exposure to hunting or trapping could reduce sightings. Although wolves show preference for linear travel corridors (James & Stuart-Smith 2000) and roads with low levels of traffic (Thurber et al. 1994; Ciucci et al. 2003), wolves will avoid of high levels of human activity (Theuerkauf et al. 2003; Whittington et al. 2005; Hebblewhite & Merrill 2008). However, the direct link between exposure to harvest and subsequent behavioral avoidance leading to reduction in sightings was not explicitly tested in our analysis. Monitoring behavior of wolves that survive negative encounters with humans is needed to determine the strength of these anti-predatory responses.

Selection for behavioral traits may be another method by which harvest of wolves could decrease sightings. Harvest can selectively target 'bold' individuals (Ciuti et al. 2012; Madden & Whiteside 2014), thereby removing bold individuals and over time, the trait, from populations. Indeed, phenotypic changes driven by human harvest can outpace selection of traits driven by other forces (Darimont et al. 2009). As wolves that are less wary may contribute disproportionately to wolf viewing opportunities, sightings could decrease if harvest selects these individuals.

We hypothesized that harvest of breeding wolves would disproportionately influence sightings, because these individuals play an important role in pack continuity and reproduction (Brainerd et al. 2008; Borg et al. 2015) and were more likely to be near the road than non-breeding wolves (Borg et al., unpublished). Although harvest reduced sightings, the breeding status of harvested wolves was not identified as an important factor in our analyses (Table 3.1). Instead, our results suggest that harvest of wolves from road packs has a larger influence on sightings than harvest of other wolves. Sightings were not reduced in YNP following the harvest of 2 wolves that were not members of road packs. These wolves resided in the park but likely contributed little to sightings as they did not live along the road corridor. However, our results from YNP were based on a limited sample size. We recommend continued monitoring of wolf sightings and increased emphasis on identifying age, reproductive status and pack affiliation for wolves harvested adjacent to protected areas to increase our understanding of these influences on wolf sightings.

Collared wolves made up over half of the harvest adjacent to YNP while comprising approximately a quarter of wolves in the YNP population, whereas collared wolves were harvested in proportion to their occurrence in the DNPP population. A major difference among these parks is that harvest near YNP is through hunting whereas harvest near DNPP is primarily through trapping. Although both harvest methods have the potential to act as selective forces on behavioral traits (i.e. bold or unwary individuals), hunting involves more active selection by humans whereas trapping passively selects wolves. This distinction could explain why there was disproportional harvest of collared wolves adjacent to YNP and not adjacent to DNPP if hunters targeted collared wolves. It is important to note that results from YNP were based on three years of data, and longer term analysis could yield different results. Still, the disproportional harvest of collared wolves may be a mechanism by which wolf sightings decrease following harvest, as the presence of collared wolves aids in locating wolves and creating viewing opportunities (R. McIntyre, pers. obs.).

In both parks, the number of identified breeders that were harvested was not different than expected given their proportion in the population. We expected that breeders would be less likely to be harvested, particularly when trapping was the primary source of harvest, as in DNPP (Adams et al. 2008). It is possible that the benefit of experience and age in avoiding trapping may be offset in protected regions by habituation to human activity and use of linear travel corridors during the summer months (Thurber et al. 1994). Given that the primary source of harvest was hunting, the result in YNP is consistent with previous findings (Peterson et al. 1984; Ballard et al. 1987; Adams et al. 2008).

The presence of the trapping and hunting buffer zone was associated with increased wolf sightings in DNPP. Both the wolf population size and PNRI, which were strongly associated with increased wolf sightings, were also greater during the period when the buffer zone was in place. Thus, the presence of the buffer may have influenced local population size and the likelihood that wolves would den near the park road. Alternatively, the increase in sightings may have been a result of coincidental peaks in population size or PNRI as a result of variables not measured or explicitly included in our models. Two variables generally considered to be strong drivers of wolf population dynamics are prey density and snow conditions, which influence prey vulnerability to wolf predation (Mech et al. 1998). However, during the period of the study, prey densities were relatively consistent (Adams & Roffler 2009; Owen & Meier 2009; Schmidt & Rattenbury 2013). Similarly, although snow conditions varied among years, there has been no statistically significant trend in the annual snowfall data for park headquarters over the past 20 years (NOAA 2015). Similarly in YNP, neither climatic conditions nor prey base were thought to significantly alter wolf population dynamics in YNP during the study period. The elk population was stable during the study time period, and although snow depth in winter 2010-2011 was above average, the other winters were within the average range for snowfall and temperature (Western Regional Climate Center 2015).

The opportunity to view free ranging large carnivores is an important driver for wildlife tourism worldwide, and the National Park Service mission in particular emphasizes the preservation of wildlife resources in their natural condition for the non-consumptive benefit and enjoyment of the public. Thus, factors that influence sightings of iconic wildlife such as wolves are important to track and understand. Here, we have shown that consumptive use of wolves reduces opportunities for non-consumptive use in protected areas. Limiting wolf harvest along the boundaries of protected areas may provide a strategy to increase wolf sighting opportunities for park visitors and the associated economic benefits to adjacent communities. However, there are associated costs of limiting harvest, given the revenue generated from wolf hunting (Montana Fish, Wildlife and Parks 2011; Idaho Fish and Game 2015) and the potential of harvest to reduce threats to livestock and increase land owner's acceptance of wolves (Mech 2010). Cross boundary wolf movements will continue to make wolf management an on-going source of debate. Effective wolf management in areas where cross boundary movements are common requires knowledge of complex system dynamics, in addition to understanding and defining the objectives of stakeholders, and quantifying the associated costs and benefits of management actions.

3.6 Acknowledgements

Funding was provided by the National Park Service and the US Geological Survey, National Science Foundation grant DEB-1245373, the Yellowstone Park Foundation, an anonymous donor, B. Graham, A. Graham, F. Yeager and K. Yeager. L. D. Mech, L. Adams, J. Burch, B. Dale and T. Meier pioneered the long term study wolf study in Denali National Park and Preserve and collected data from 1986 to 2012. J. Drain, R. Rausch diligently reviewed and summarized YNP sighting data. S. Brainerd, J. Falke, G. Hilderbrand, and M. Lindberg provided valuable comments on earlier versions of this manuscript. Capture and handling protocols were approved by the National Park Service Institutional Animal Care and Use Committee and are in accordance with recommendations from the American Society of Mammalogists (Sikes et al. 2011). Work was conducted under annual National Park Service permits, annual State of Alaska Department of Fish and Game scientific permits, and the University of Alaska permit (253217-3). Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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3.8 Figures

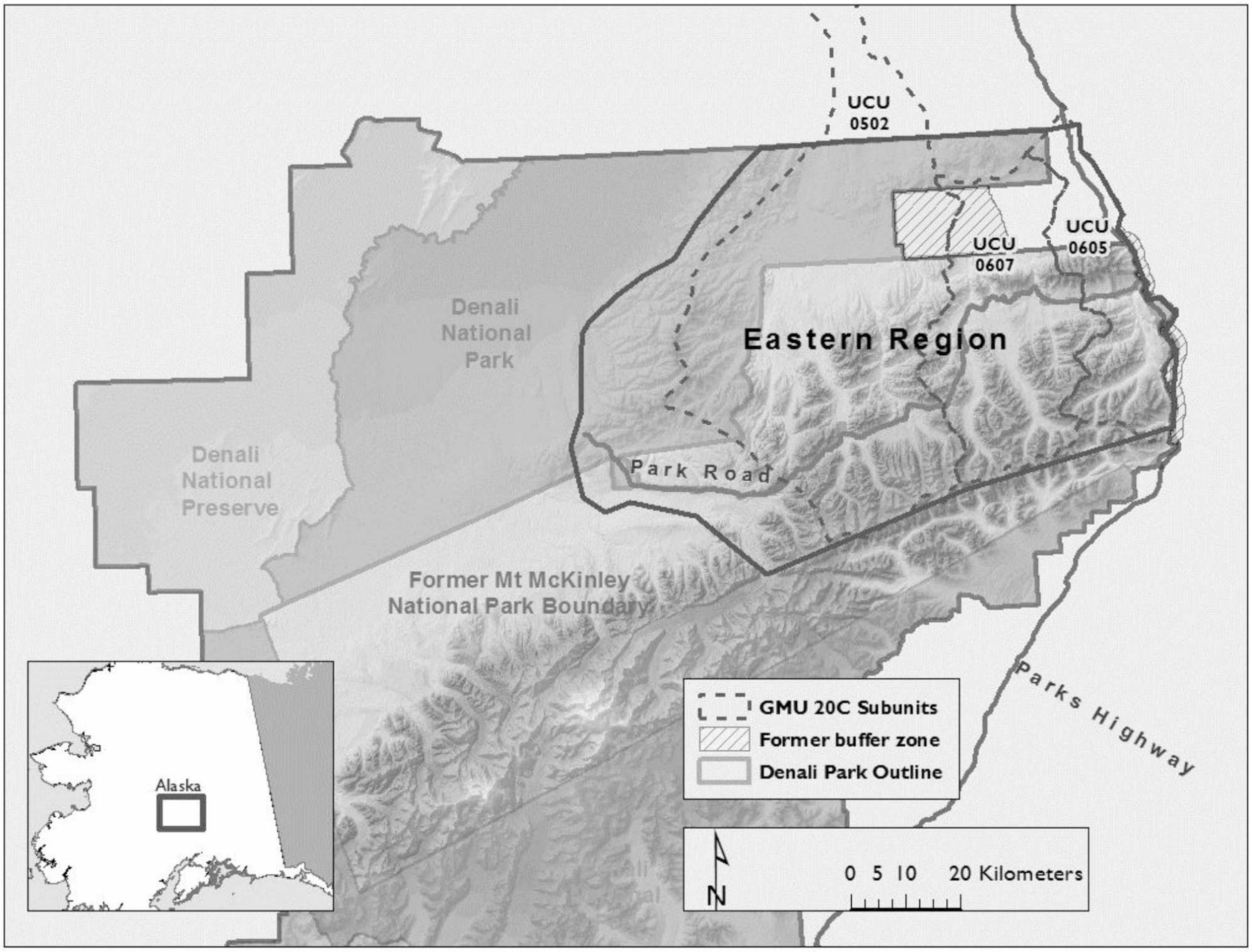

Figure 3.1. Map of study area and geographical sub-population regions for long term monitoring of grey wolf packs in Denali National Park and Preserve, Alaska, USA. Uniform Coding Units (UCUs) within Game Management Unit 20C and former buffer zone where wolf hunting and trapping was prohibited from 2000 to 2010 are shown.

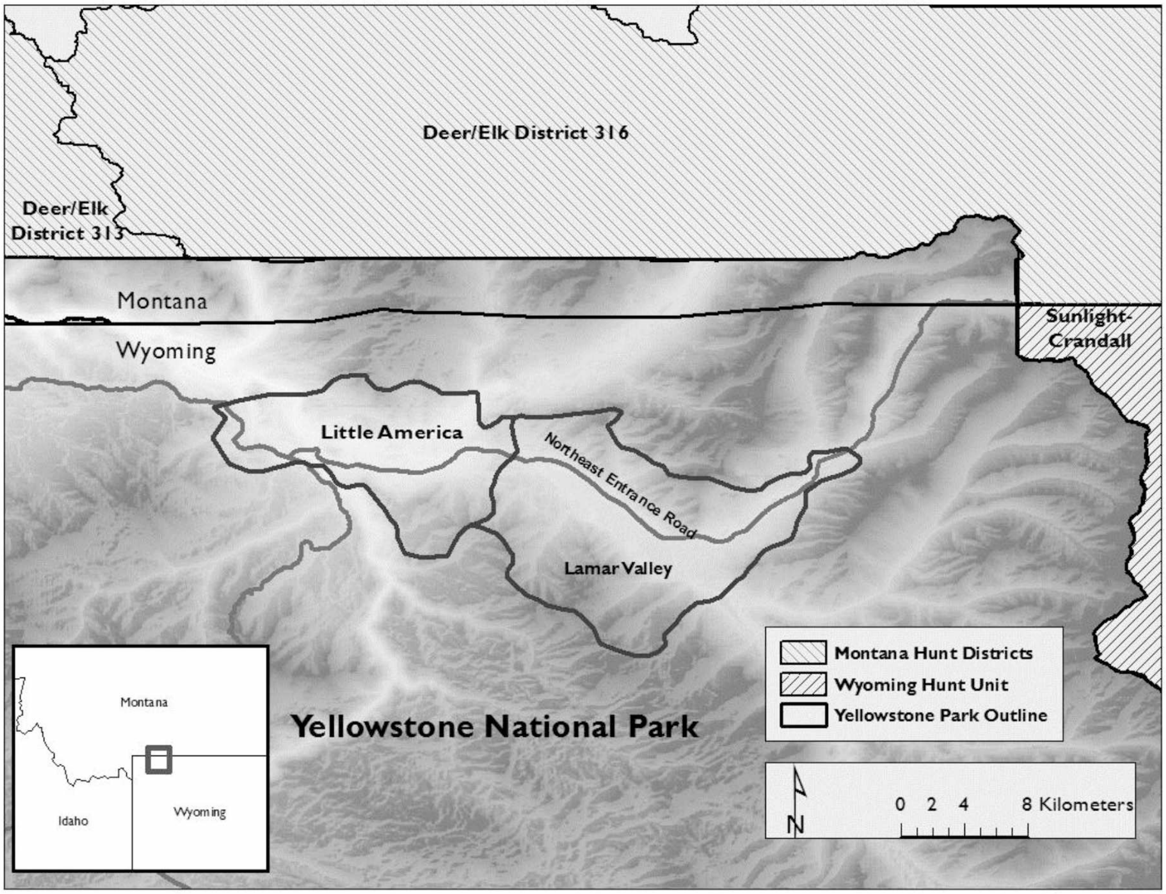

Figure 3.2. Map of study area and sighting sections within the Northern Range of Yellowstone National Park, Wyoming, USA.

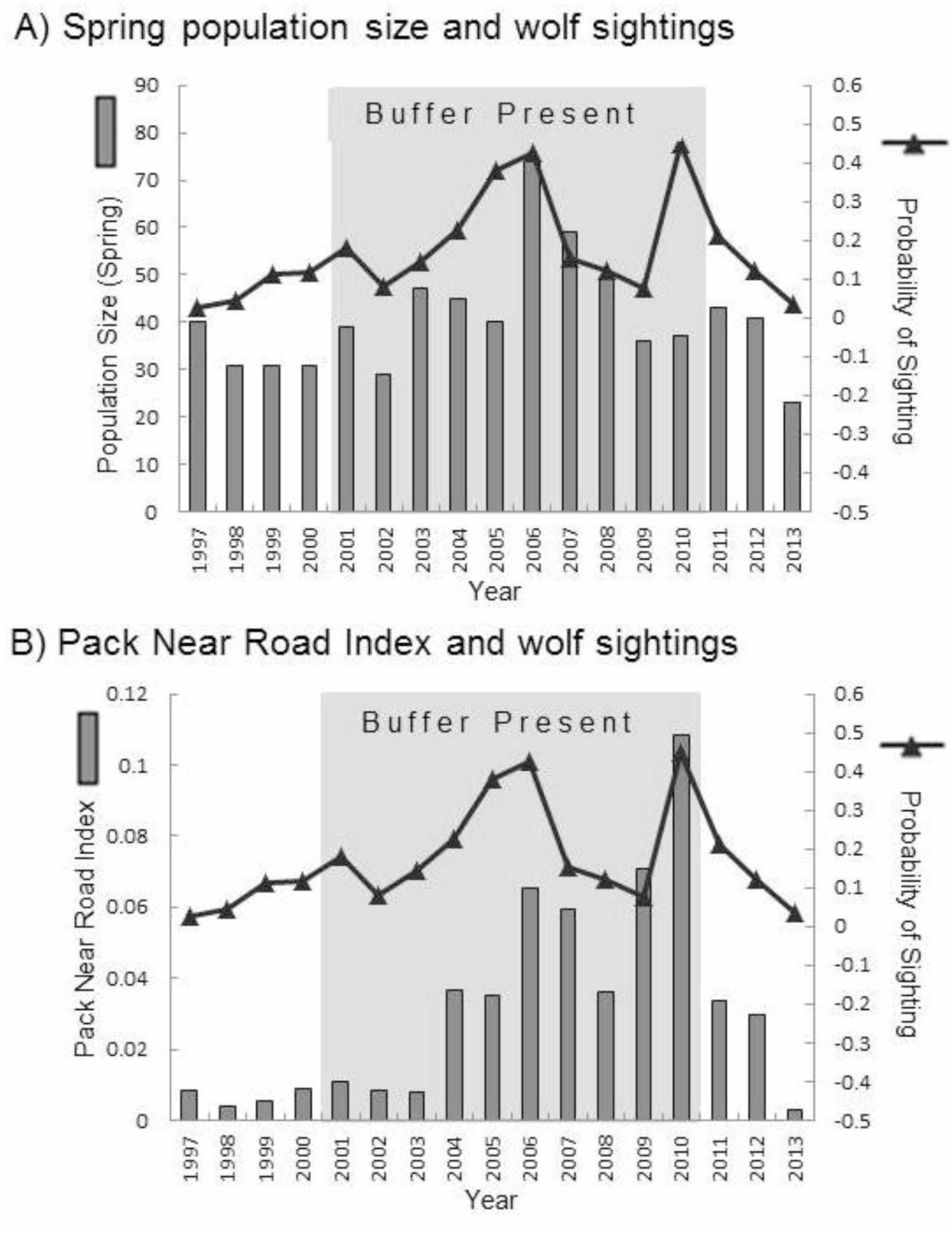

Figure 3.3. Probability of wolf sighting along the Denali Park Road from 1997 to 2012 (black triangles) in relation to A) spring population size (gray bars) and B) the Pack Near Road Index (number of wolves in road packs divided by den distances from the road, gray bars) in Denali National Park and Preserve, Alaska, USA. Shaded areas indicate the time period (2000-2010) when a harvest buffer zone adjacent to the park was in effect.

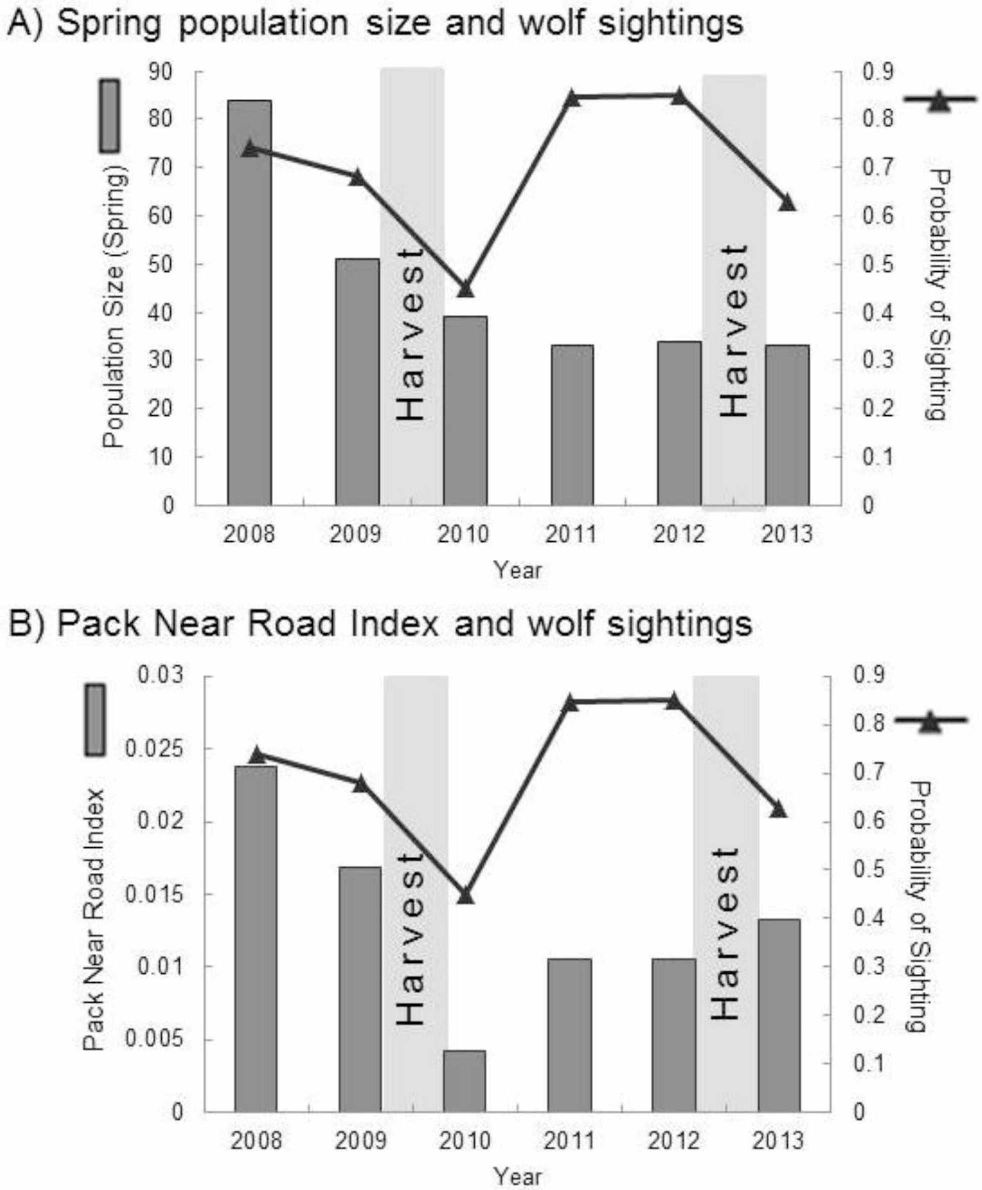

Figure 3.4. Probability of wolf sighting in Little America and Lamar Valley from 2008-2012 (black triangles) in relation to A) spring population size and B) Pack Near Road Index (number of wolves in road packs divided by den distances from the road) in Yellowstone National Park, Wyoming, USA. Shaded areas indicate years following harvest of wolves from packs. Two non-pack wolves were harvested prior to 2011.

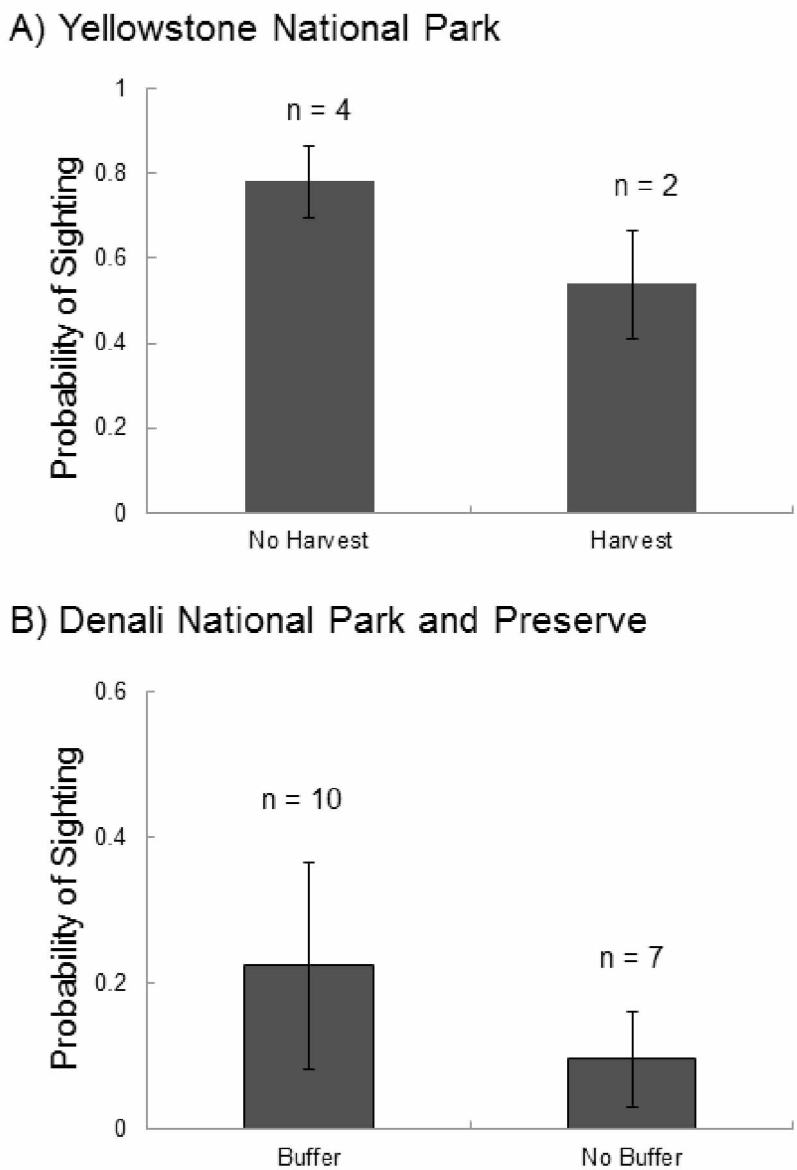

Figure 3.5. Mean probability of sighting for wolves A) in Lamar Valley and Little America following years with and without harvest of pack wolves, Yellowstone National Park, Wyoming, USA and B) along the Denali Park Road following years with and without the presence of a buffer zone prohibiting the trapping and hunting of wolves outside of Denali National Park and Preserve, AK, USA. Standard error bars and sample sizes (number of years) are shown.

3.9 Tables

Table 3.1. Candidate model set and model selection criteria evaluating factors potentially affecting probability of wolf sightings along Denali Park Road in Denali National Park and Preserve, Alaska, USA. K is the number of parameters in the model, PNRI is the Pack Near Road Index, TotalPop is the population size, Buffer is a factor indicating the presence/absence of a harvest buffer, WolfHarv is the number of wolves harvested in the prior year and BreedHarv is a factor if breeders were or were not harvested from road packs in the prior year.

Model	K	AICc	ΔAICc	Model Likelihood	AICc Weight	Pseudo R^2
PackNearRoad+Buffer+WolfHarv	4	154.34	0.00	1.00	1.00	0.67
PackNearRoad+Buffer	3	175.72	21.39	0.00	0.00	0.55
PackNearRoad+Buffer+BreedHarv	4	178.47	24.13	0.00	0.00	0.55
TotalPop+Buffer+WolfHarv	4	187.78	33.44	0.00	0.00	0.51
TotalPop+Buffer+BreedHarv	4	188.19	33.85	0.00	0.00	0.51
PackNearRoad+WolfHarv	3	189.54	35.20	0.00	0.00	0.48
TotalPop+Buffer	3	196.43	42.09	0.00	0.00	0.45
PackNearRoad	2	198.63	44.30	0.00	0.00	0.43
PackNearRoad+BreedHarv	3	199.70	45.36	0.00	0.00	0.44
Buffer	2	212.27	57.94	0.00	0.00	0.36
TotalPop+BreedHarv	3	213.99	59.66	0.00	0.00	0.37
TotalPop	2	238.72	84.38	0.00	0.00	0.24
TotalPop+WolfHarv	3	240.84	86.51	0.00	0.00	0.24
WolfHarv	2	284.58	130.25	0.00	0.00	0.02

Table 3.2. Parameter estimates for annual probability of sighting model evaluating factors potentially affecting probability of wolf sightings along Denali Park Road in Denali National Park and Preserve, Alaska, USA. PNRI is the Pack Near Road Index, Buffer is the presence of a wolf hunting and trapping buffer and WolfHarv is the number of wolves harvested in surrounding regions.

Parameter	β	SE	95% CL	
			Lower	Upper
(Intercept)	-2.6	0.15	-2.89	-2.31
PNRI	24.6	3.13	18.47	30.73
Buffer (Presence)	1.0	0.17	0.70	1.36
WolfHarv	-0.11	0.02	-0.15	-0.07

Table 3.3. Mean estimates (and SE), test statistics, and *P*-values for the annual probability of wolf sighting, wolf population, and Pack Near Road Index (PNRI) for years following the presence (2001-2010) and absence (1997-2000, 2011-2013) of a hunting and trapping buffer adjacent to Denali National Park and Preserve, AK, USA.

	Buffer	**No Buffer**	t_{15}	***P*-value**
Sightings	0.22 (0.142)	0.10 (0.066)	2.2	0.02
Population	45.5 (12.98)	34.3 (7.23)	2.1	0.03
PNRI	0.04 (0.032)	0.01 (0.013)	2.4	0.02

3.10 Supporting Information

Appendix S3-1. Recording Wildlife Sightings in Denali National Park and Preserve

Observers recorded all sightings of 5 large mammal species: grizzly bear, caribou, Dall Sheep, moose, and wolves. Data recorded included: date, time, species, number of adults and young, animal's distance from the road and location of sighting. Bus drivers collected written observations on wildlife sightings along the park road from 1995 to 2007 following standard protocols (Tomkiewicz et al. 1999). From 2006 to 2013, panels linked to mobile GPS units mounted in buses allowed bus drivers to record and classify wildlife stops along the DPR. Stops were categorized by species (grizzly bear, caribou, Dall Sheep, moose, wolf, or other) and panel entries were linked to locations of the bus by a mobile GPS unit mounted in each bus (Validator V2000, Universal Tracking, Valencia, CA, USA and Fleet Management System, San Luis Obisbo, CA, USA). Additionally, from 2007-2013, DNPP biological staff members conducted formal surveys of wildlife observed along the park road to validate driver collected data and record additional information on wildlife behavior. From 2010-2013, NPS staff used Juno SB handheld GPS receivers with TerraSync software (Trimble, Sunnyvale, CA, USA) to collect wildlife observation data. The same data were collected as in previous years.

We used two methods to compare data collected by bus drivers and NPS staff in DNPP in 2011. First, we used a proportional population z-test to compare the proportion of trips seeing one or more wolves (probability of sighting) on a trip to Eielson Visitor Center at mile 66 (Fig.3.1). Second, we used a t-test to compare the mean number of groups (individual or more than one) of each species seen by the two methods. The two wolf sighting metrics were not statistically different between two collection methods. The probability of sighting for bus driver data was 0.16 (SE 0.007) and for NPS staff was 0.21 (SE 0.021, $\chi 2=0.62$, df=1, P=0.43). The average number of groups of wolves seen based on bus driver data was 0.20 (SE 0.025) and for NPS staff data was 0.34 (SE 0.102, P=0.1728). We therefore combined the data collected by bus drivers from 1997 to 2009 and DNPP staff from 2010-2013 for subsequent analysis.

Appendix S3.2. Additional Figures and Table

Table S3.1. Population size estimates, number of collared wolves, number of collared breeding wolves, and their proportions in the population and harvest for the Eastern Region of Denali National Park and Preserve, AK, USA. Population size, number of collared wolves, and number of collared breeders were pre-hunt numbers.

Regulatory Year	Fall Population Size	Packs	Collared Wolves	Collared Breeders	Harvest	Collared Harvest	Collared Breeder Harvest	Proportion of Pop Collared	Proportion Harvest Collared	Diff	Proportion Collared Breeders in Pop	Proportion Collared Breeders in Harvest	Diff
1996	49	6	16	9	4	1	0	0.33	0.25	0.08	0.24	0.00	0.24
1997	44	7	22	13	1	1	1	0.50	1.00	-0.50	0.32	1.00	-0.68
1998	35	8	17	11	0	0	0	0.49	NA	NA	0.46	NA	NA
1999	43	8	17	12	1	1	0	0.40	1.00	-0.60	0.37	0.00	0.37
2000	49	8	19	13	6	0	0	0.39	0.00	0.39	0.33	0.00	0.33
2001	45	9	19	13	1	0	0	0.42	0.00	0.42	0.40	0.00	0.40
2002	55	11	14	9	6	0	0	0.25	0.00	0.25	0.40	0.00	0.40
2003	55	9	13	9	9	6	5	0.24	0.67	-0.43	0.33	0.56	-0.23
2004	49	9	12	7	3	1	1	0.24	0.33	-0.09	0.37	0.33	0.03
2005	77	9	13	4	3	1	1	0.17	0.33	-0.16	0.23	0.33	-0.10
2006	75	9	18	5	9	1	0	0.24	0.11	0.13	0.24	0.00	0.24
2007	84	10	22	11	11	3	2	0.26	0.27	-0.01	0.24	0.18	0.06
2008	56	9	17	12	8	2	1	0.30	0.25	0.05	0.32	0.13	0.20
2009	57	8	12	9	11	1	1	0.21	0.09	0.12	0.28	0.09	0.19
2010	53	6	12	7	3	1	0	0.23	0.33	-0.11	0.23	0.00	0.23
2011	45	5	13	9	3	1	1	0.29	0.33	-0.04	0.22	0.33	-0.11
2012	29	4	10	7	2	0	0	0.34	0.00	0.34	0.28	0.00	0.28

Table S3.2. Population size estimates, number of collared wolves, number of collared breeding wolves, and their proportions in the population and harvest for Northern Range packs (including Mollie's pack), Yellowstone National Park, Wyoming, USA. Population size, number of collared wolves, and number of collared breeders were pre-hunt numbers.

Regulatory Year	Fall Population Size	Packs	Collared Wolves	Collared Breeders	Harvest	Collared Harvest	Collared Breeder Harvest	Proportion of Pop Collared	Proportion Harvest Collared	Diff	Proportion Collared Breeders in Pop	Proportion Collared Breeders in Harvest	Diff
2009	66	8	21	13	4	2	1	0.32	0.50	-0.18	0.20	0.50	-0.30
2011	74	4	17	5	2	1	0	0.23	0.50	-0.27	0.07	0.00	0.07
2012	57	5	15	5	9	5	1	0.26	0.56	-0.29	0.09	0.11	-0.02

Table S3.3. Population size estimates, number of collared wolves, number of collared breeding wolves, and their proportions in the population and harvest in Yellowstone National Park, Wyoming, USA. Population size and number of collared wolves were pre-hunt numbers.

Regulatory Year	Fall Population Size	Packs	Collared Wolves	Harvest	Collared Harvest	Proportion of Pop Collared	Proportion Harvest Collared	Diff
2009	128	14	36	4	2	0.28	0.50	-0.22
2011	135	11	31	2	1	0.23	0.50	-0.27
2012	99	10	27	12	7	0.27	0.58	-0.31

Table S3.4. Candidate model set and model selection criteria evaluating factors potentially affecting probability of wolf sightings along Denali Park Road in Denali National Park and Preserve, AK. Akaike information criterion corrected for sample sizes and overdispersion (QAICc). We accounted for variance inflation using an estimate of overdispersion ($\hat{c}$= 5.4) from the package MuMIn in package R (Barton 2014). K is the number of parameters in the model, PNRI is the Pack Near Road Index, TotalPop is the wolf population size, RoadPop is the number of wolves in packs that overlap the road, Buffer is a factor indicating the presence/absence of a harvest buffer, WolfHarv is the number of wolves harvested in the prior year, and BreedHarv is a binary factor describing if breeders were or were not harvested from road packs in the prior year.

Model	K	QAICc	ΔQAICc	Model Likelihood	QAICc Weight	Quasi LogLikelihood
PackNearRoad+Buffer+WolfHarv	4	41.70	0.00	1.00	0.33	-71.50
PackNearRoad+Buffer	3	42.15	0.44	0.80	0.27	-83.94
PackNearRoad	2	43.42	1.71	0.43	0.14	-96.89
PackNearRoad+WolfHarv	3	44.68	2.98	0.23	0.07	-90.85
Buffer	2	45.92	4.22	0.12	0.04	-103.71
TotalPop+Buffer	3	45.95	4.25	0.12	0.04	-94.29
PackNearRoad+Buffer+BreedHarv	4	46.13	4.43	0.11	0.04	-83.57
PackNearRoad+BreedHarv	3	46.55	4.85	0.09	0.03	-95.93
TotalPop+Buffer+WolfHarv	4	47.84	6.14	0.05	0.02	-88.22
TotalPop+Buffer+BreedHarv	4	47.92	6.21	0.04	0.01	-88.43
TotalPop+BreedHarv	3	49.17	7.47	0.02	0.01	-103.07
TotalPop	2	50.77	9.07	0.01	0.00	-116.93
TotalPop+WolfHarv	3	54.10	12.40	0.00	0.00	-116.50
WolfHarv	2	59.19	17.49	0.00	0.00	-139.86

Table S3.5. Model averaged parameter estimates for annual probability of sighting model evaluating factors potentially affecting probability of wolf sightings along Denali Park Road in Denali National Park and Preserve, AK. PNRI is the Pack Near Road Index, Buffer is the presence of a wolf hunting and trapping buffer and WolfHarv is the number of wolves harvested in surrounding regions. Model averaged parameter estimates were obtained using model weights from QAICc model selection and variance inflation using an estimate of overdispersion (ĉ= 5.4) from the package MuMIn in package R (Barton 2014).

Parameter	β (Model Averaged)	SE	95% CL	
			Lower	Upper
(Intercept)	-2.7	0.11	-2.90	-2.48
PNRI	22.8	8.46	6.26	39.41
Buffer (Presence)	1.0	0.47	0.08	1.84
WolfHarv	-0.1	0.06	-0.21	0.01

Table S3.6. Candidate model set and model selection criteria evaluating factors potentially affecting probability of wolf sightings along Denali Park Road in Denali National Park and Preserve, AK, including the factor RoadPop in the model set. (K is the number of parameters in the model, PNRI is the Pack Near Road Index, TotalPop is the wolf population size, RoadPop is the number of wolves in packs that overlap the Denali Park Road, Buffer is a factor indicating the presence/absence of a harvest buffer, WolfHarv is the number of wolves harvested in the prior year and BreedHarv is a binary factor describing if breeders were or were not harvested from road packs in the prior year.

Model	K	AICc	ΔAICc	Model Likelihood	AICc Weight	Log Liklihood	Pseudo R^2
PackNearRoad+Buffer+WolfHarv	4	154.34	0.00	1.00	1.00	-71.50	0.67
PackNearRoad+Buffer	3	175.72	21.39	0.00	0.00	-83.94	0.55
PackNearRoad+Buffer+BreedHarv	4	178.47	24.13	0.00	0.00	-83.57	0.55
TotalPop+Buffer+WolfHarv	4	187.78	33.44	0.00	0.00	-88.22	0.51
TotalPop+Buffer+BreedHarv	4	188.19	33.85	0.00	0.00	-88.43	0.51
PackNearRoad+WolfHarv	3	189.54	35.20	0.00	0.00	-90.85	0.48
TotalPop+Buffer	3	196.43	42.09	0.00	0.00	-94.29	0.45
PackNearRoad	2	198.63	44.30	0.00	0.00	-96.89	0.43
PackNearRoad+BreedHarv	3	199.70	45.36	0.00	0.00	-95.93	0.44
RoadPop+Buffer+BreedHarv	4	209.64	55.31	0.00	0.00	-99.15	0.41
Buffer	2	212.27	57.94	0.00	0.00	-103.71	0.36
TotalPop+BreedHarv	3	213.99	59.66	0.00	0.00	-103.07	0.37
RoadPop+Buffer+WolfHarv	4	214.70	60.36	0.00	0.00	-101.68	0.38
RoadPop+Buffer	3	215.23	60.90	0.00	0.00	-103.69	0.36
TotalPop	2	238.72	84.38	0.00	0.00	-116.93	0.24
TotalPop+WolfHarv	3	240.84	86.51	0.00	0.00	-116.50	0.24
RoadPop+BreedHarv	3	264.62	110.29	0.00	0.00	-128.39	0.13
WolfHarv	2	284.58	130.25	0.00	0.00	-139.86	0.02
RoadPop+WolfHarv	3	287.57	133.23	0.00	0.00	-139.86	0.02
RoadPop	2	288.00	133.67	0.00	0.00	-141.57	0.01

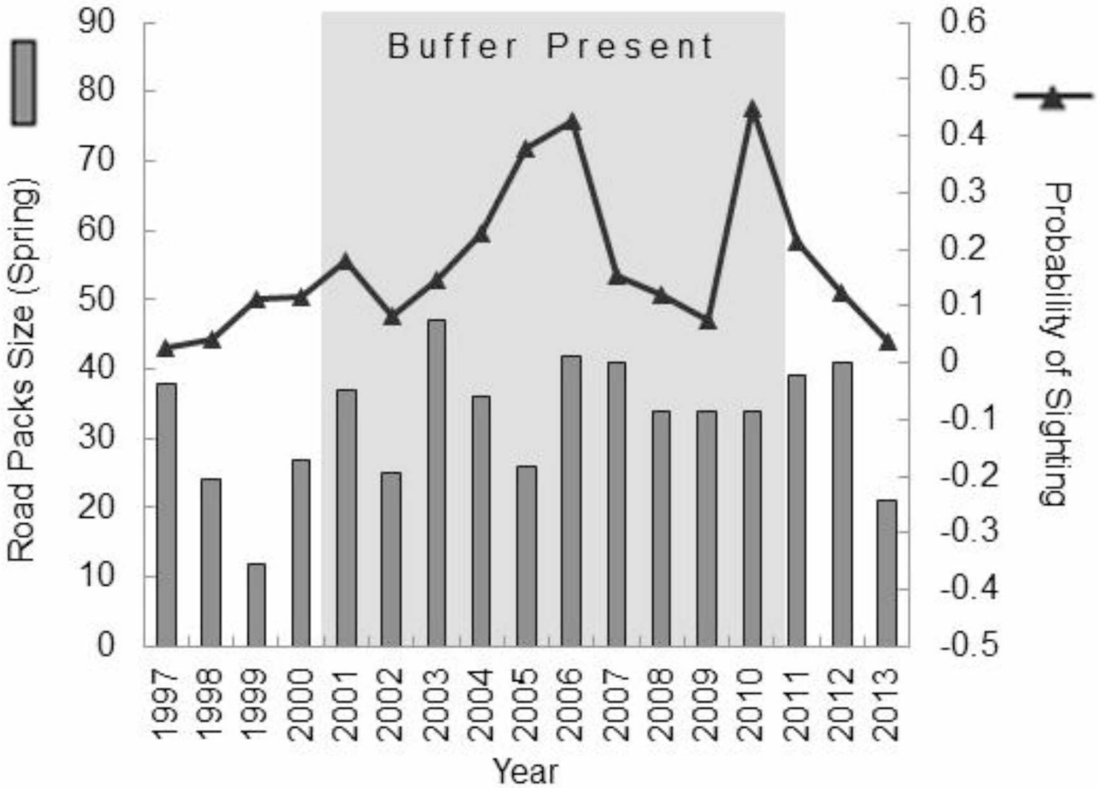

Figure S3.1. Cumulative count of wolves in road packs in the eastern region of Denali National Park and Preserve (grey bars) and the probability of wolf sightings along the Denali Park Road (black triangles) from 1997 to 2012. Shading indicates years with a harvest buffer zone adjacent to the park in effect.

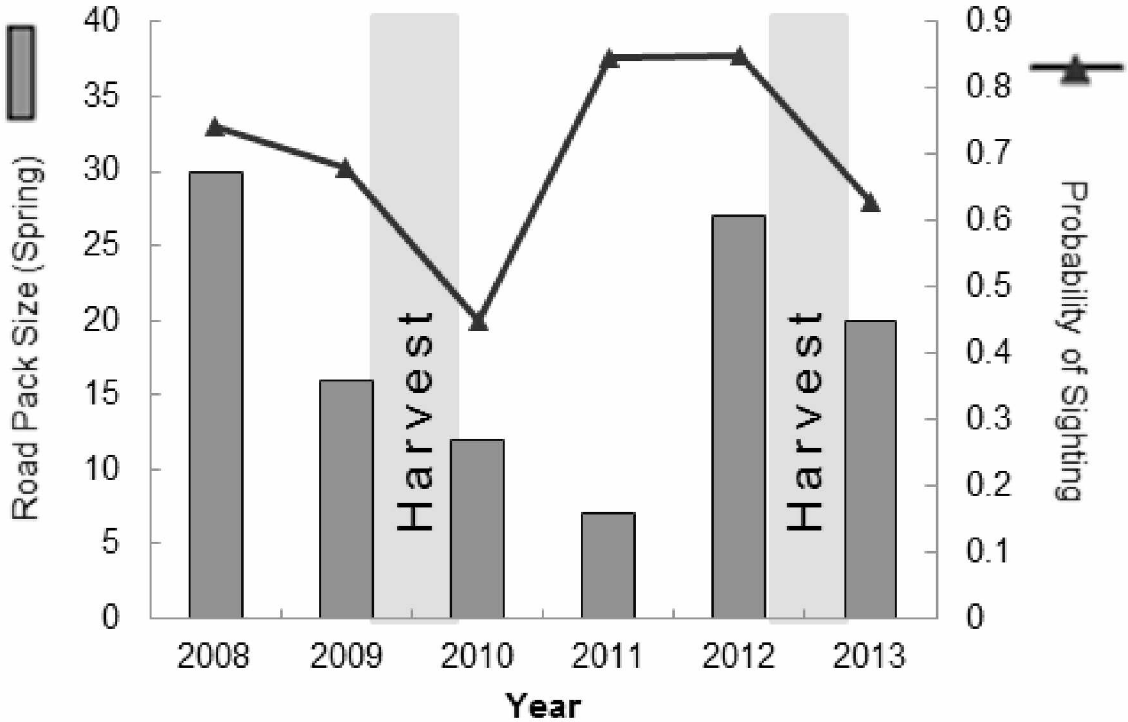

Figure S3.2. Cumulative count of wolves in road packs in the Northern Range of Yellowstone National Park (grey bars) and probability of wolf sightings in Little America and Lamar Valley (black triangles) from 2008-2012. Hashed bars indicate years preceded by harvest of wolves from road packs. Light gray shading indicates years preceded by harvest of non- pack wolves.

Chapter 4

Dynamics of wolf sightings in Denali National Park[1]

4.1 Abstract

Wildlife viewing within protected areas is an increasingly popular recreational activity, and agencies are often tasked with providing these opportunities as an important component of visitor experience. Despite the importance of wildlife viewing in protected areas, quantitative analyses of factors that influence wildlife sightings are lacking. Here, we used data from GPS collared wolves from 2004 - 2012 to examine the factors that influence the probability of a wolf being in an observable area of the Denali Park Road in Denali National Park, Alaska, and we used spatially-explicit data on wolf sighting locations from 1997-2013 to evaluate how wolf sightings varied along road sections in relation to physical, biological and harvest characteristics. We found that den distance, den success, and pack size influenced both the probability of wolf presence near the road and the probability of sightings. Predictably, the presence of masking vegetation alongside the road corridor decreased wolf sightings and den site proximity to the road had a strong effect on sightings, particularly when dens were very close to the road. The presence of a wolf harvest buffer zone adjacent to the park also increased wolf sightings along the Denali Park Road. The effect of the harvest buffer on sightings was similar in magnitude to an increase in pack size by two wolves or a more than a two-fold decrease in masking vegetation (Table 4.5). Our results suggest that harvest adjacent to parks, disturbance of den sites, and increased vegetation along park roads all have the potential to substantially reduce wolf sightings. Quantitative analysis of the factors influencing wildlife sightings provides valuable insight for agencies tasked with managing for visitor experience related to these opportunities.

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[1] Prepared for submission to PLOS ONE Borg, B.L., S.M. Arthur, J. A. Falke., and L. R. Prugh. 2015. Dynamics of wolf sightings in Denali National Park.

4.2 Introduction

Wildlife viewing is one of the most popular outdoor recreational activities in the United States. Approximately 1 in 3 people over the age of 16 participate in wildlife viewing activities each year, and people spent over 54 billion dollars on wildlife viewing activities in the U.S. in 2011 alone (U. S. Department of the Interior et al. 2011). Protected areas such as national parks and monuments are destinations for people seeking opportunities to view wildlife in natural settings, and responsible agencies are often mandated to protect wildlife viewing opportunities as an important component of visitor experience (Manfredo 2002).

Denali National Park and Preserve (DNPP) is a popular wildlife viewing destination in interior Alaska, with over 400,000 visitors each year (Fix et al. 2012). DNPP management documents define "the possibility of observing free-roaming wildlife at close range in a rugged wilderness setting" as a key feature of the park (Denali National Park and Preserve 1995). Indeed, many visitors come to DNPP specifically for the opportunity to observe wildlife, including grizzly bears (*Ursus arctos),* moose (*Alces alces*), caribou (*Rangifer tarandus*), Dall sheep (*Ovis dalli dalli*), and wolves (*Canis lupus)* along the Denali Park Road (Manning & Hallo 2010).

While viewing any of one of the five large mammal species in DNPP is a valued experience for visitors (Skibins et al. 2012), observing wolves in the wild is particularly uncommon and highly valued (Montag et al. 2005). Indeed, DNPP is one of the best places in the world to see wolves in their natural habitat. In some years, over 20,000 visitors may observe wolves along the Denali Park Road (Borg, unpublished). Several packs in the eastern portion of the park occupy territories that often span the road corridor. The proximity of these packs to the road provides viewing opportunities to park visitors. However, low wolf population estimates combined with the abolition of a "closed area" where wolf hunting and trapping was prohibited adjacent to DNPP in spring 2010 raised a series of concerns over the impact these factors could have on wolf sighting opportunities for DNPP visitors (Hooge 2010).

A number of studies in DNPP have documented wildlife sightings and wildlife behavior along the Denali Park Road since the 1980s (Singer et al. 1986; Taylor et al 1997; Looney 1992; Burson et al. 2000; Yost & Wright 2001). However, quantitative analysis has focused on grizzly bear, moose, caribou and Dall sheep sightings in relation to traffic levels (Singer et al. 1986; Burson et al. 2000), which have been regulated and relatively constant since 1986 (National Park Service 1986). Despite the importance of wolf sightings to park visitors, a quantitative analysis of factors that influence wolf sightings along the Denali Park Road was lacking.

Our objective was to improve our understanding of the topographic and biotic factors that influence the probability of seeing a wolf along the Denali Park Road. First, we used data from GPS collared wolves to examine factors that influence the probability of a wolf being in an observable area (within 500 m) of the park road. The goal of this analysis was to improve our understanding of how characteristics of individual wolves and packs may influence wolf viewing opportunities. We hypothesized that den site location, breeding status of individual wolves, and pack size would influence wolf movement patterns. We predicted that the probability of a wolf being near the road would increase with increasing proximity of a wolf den site to the road, as wolves' movements radiate from a central den site location in the summer (Packard 2003). We also predicted that breeders would have a lower probability of being in an observable area than non-breeders, because breeders may be more likely to attend to pups and remain near den sites (Thurston 2002; Tsunoda et al. 2009 but see Potvin et al. 2004). Den site attendance and associated movements are also influenced by pack size (Ballard et al. 1991; Tsunoda et al. 2009), and we expected that larger packs would increase the probability of a wolf being located near the road because additional wolves would be foraging and individuals could have longer foraging bouts (Ruprecht et al. 2012). Additionally, we expected that failed recruitment (i.e., denning failure or early mortality of pups) would decrease the probability of wolf presence near the road because movements would no longer be tied to the den site.

Next, we evaluated how wolf sightings along the Denali Park Road varied with physical, biological and harvest characteristics. We used spatially-explicit data on wolf sighting locations from 1997-2013 to evaluate factors that influenced the probability of a wolf being near the road and the detectability of a wolf in a given section of road. We hypothesized that factors increasing the probability of a wolf being near the Denali Park Road would increase sightings along the road corridor as well. In addition, we hypothesized that harvest of wolves adjacent to the park would reduce sightings, and that topography and vegetation along the road corridor would influence the detection of wolves.

4.3 Methods

4.2.1 Study areas

The study area encompassed approximately 6,350 km^2 of wolf habitat primarily north of the Alaska Range in and adjacent to DNPP (Fig. 4.1). This region of DNPP contains patches of boreal forest, high alpine, braided rivers, and willow-lined creeks. The diversity of habitat types in the region supports caribou, Dall sheep, and moose populations (Mech et al. 1998; Adams & Roffler 2009; Owen & Meier 2009). The climate is subarctic, with short, cool summers ranging on average from 0° to 24° C (Western Regional Climate Center 2007). Annual precipitation averages 38 cm with over half occurring during the summer months. Snow cover is generally present from October through early May. From 1997-2013, cumulative winter snowfall (September- April) ranged from 27-296 cm (mean = 150 ± 69 cm). The study area is bisected by the Denali Park Road (Fig. 4.1), which provides visitor access to the region and the majority of wolf viewing opportunities.

4.2.2 Data collection

4.2.2.1 Population monitoring and pack counts

Wolf population monitoring efforts and use of radio-telemetry for tracking and monitoring packs began in 1986 (Mech et al. 1998). From 1986 to 2012, 387 individual wolves were instrumented with very high frequency (VHF) collars (Borg & Burch 2014). From 2003 to 2012, 30 of the VHF collars were equipped with GPS (Telonics, Mesa, CA), which provided one or more daily locations (Meier et al. 2009). Wolves were immobilized by darting from helicopters and collared following established protocols (Meier et al. 2009; Sikes et al. 2011). Wolf project staff used a combination of aerial and ground monitoring techniques to collect data on wolf locations, numbers of pack members, active den site locations and use, and breeding status of individual wolves (Mech et al. 1998; Meier et al. 2009).

4.2.2.2 Den Site Locations

DNPP's wolf management plan objectives require closing areas around known den sites to hikers (National Park Service 2007). Thus, den site locations and use were closely monitored for wolf packs in areas along the road corridors. Data on denning status of packs, as well as den site locations, were gathered by field personnel on foot or during aerial observation and recorded on handheld GPS units (Garmin, Olathe, KS, USA). We determined the distance of den sites to the nearest location on the Denali Park Road using the "near" tool in ArcGIS version 10.2 (ESRI 2011, ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute).

4.2.2.3 Harvest

Wolf harvest management varied throughout the study region and the study period. All areas outside the DNPP boundary were open to hunting and trapping under state regulation, with the exception of a trapping buffer zone originally approved by the Alaska Board of Game (AKBOG) in 2000 and expanded in 2001 and 2002 (Fig. 4.1). This buffer was removed by the AKBOG in 2010. Open seasons and bag limits (i.e., the annual number of wolves that could be harvested per person per year) were managed by Alaska Department of Fish and Game (ADF&G). In Game Management Units (GMU) 20A and 20C adjacent to the park's boundaries, the hunting season was August 10 – April 30 from regulatory year 1996-1997 through 2005-2006 and extended until May 31 starting in 2006-2007. The bag limit was 10 wolves through 2001-2002, after which it was decreased to 5 wolves per season. The wolf trapping season spanned November 1– April 30 in GMUs 20A and 20C, with no bag limits for either unit. Subsistence and sport hunting and trapping were permitted in the Preserve and new park additions of DNPP, but all hunting and trapping was prohibited in the area of the original Mt. McKinley National

Park (Fig.4.1). The numbers of wolves harvested from regions adjacent to park boundaries were obtained from state harvest records and mortality of collared wolves.

4.2.2.4 Sighting data

Data on wildlife sightings along the Denali Park Road were collected during bus trips from the Savage checkpoint at mile 15 to the Eielson Visitor Center at mile 66 (Fig. 4.1). Data were collected by 1) bus drivers as written observations (1995-2007) and on electronic panels installed on buses (2007-2013) and 2) park staff and volunteers as written observations (2007-2009) and on handheld devices (2010-2013). Bus drivers collected information about wildlife viewed along the park road from 1995 to 2007 following standard protocols (Tomkiewicz et al. 1999). During westbound trips, bus drivers recorded the location, time, species, number, age, sex, and animals' distance from the road for each animal observed. Data prior to 1997 was sparse and considered pilot data. From 2006 to 2013, panels linked to mobile GPS units mounted in buses allowed bus drivers to record and classify wildlife stops along the DPR. Stops were categorized by species (grizzly bear, caribou, Dall Sheep, moose, wolf, or other). Panel entries were linked to locations of the bus by a mobile GPS unit mounted in each bus (2006-2010: Validator V2000, Universal Tracking, Valencia, CA, USA, 2011-2013: Fleet Management System, San Luis Obisbo, CA, USA).

From 2007-2013, DNPP staff conducted formal surveys of wildlife observed along the park road from mile 15 to mile 66 and recorded all sightings of wildlife, including wolves. A number of attributes were collected for each sighting including date, time, location, and distance individuals or groups were observed from the road (using a range finder or estimated visually). From 2007-

2009, staff used handheld GPS units (Garmin, Olathe, KS, USA) and paper forms to record data. From 2010-2013, staff used Juno SB handheld GPS receivers with TerraSync software (Trimble, Sunnyvale, CA, USA) to collect and record wildlife observation data.

4.2.3 Wolf Presence Model

We used the proportion of locations of collared wolves within 500 m (the maximum recorded distance a wolf was observed) of the Denali Park Road during the summer observation period (May 20- September 15) from 2004 to 2012 as the dependent variable to evaluate influences on the probability of wolf presence near the road. We included only data from wolves in packs with annual territories overlapping or within 1,500 m of the Denali Park Road for this analysis. We used the "minimum bounding geometry" tool in ArcGIS 10.2 to calculate annual pack territories as minimum convex polygons (Odum & Kuenzler 1955), excluding obvious extraterritorial forays and dispersing wolves' locations (Peterson et al. 1984) for all wolf packs in the study region. In addition, we included only GPS-collared wolves with fix acquisition rates >80%. Collars with less than 80% fix acquisition had at least one period with significant gaps in data and were thus removed from analyses.

GPS collars were programmed to collect between 1 and 8 locations daily. We investigated whether the number of daily locations collected by a collar influenced the estimate of the proportion of locations near the road. We used data from collared wolves that had the highest fix rate (8 locations per day) to compare the proportion of locations near the road estimated by sampling 1, 2, 4, 6, and 8 fixes per day. To determine if there was a statistically significant difference between the proportion of fixes near the road estimated from variable fix rates, we conducted a paired t-test on the proportion of fixes near the road calculated with 1 or 8 daily fixes.

We evaluated the covariates of den site distance from road (DenDist), spring pack size (PackSize), breeding status of wolf (WolfStatus), and denning success (Recruit) in our model set. All wolves included in our dataset were considered pack members (not loners or dispersers). DenDist was the distance of the pack's den site to the closest point on the road. We log-transformed DenDist to improve parameter estimation with maximum likelihood methods. PackSize was the size of packs recorded during annual surveys in March. Each wolf's status was classified as "breeder" or "non-breeder" based on observation of leadership behaviour, attendance at den sites, observation of nursing pups (for females) during aerial tracking, and/or through testes and nipple measurements during collaring (Mech 1999, 2000; Peterson et al. 2002; Meier et al. 2009). When breeding or dominance status was not directly recorded it was determined after thorough review of capture, mortality and aerial tracking information for each pack for all wolves in the dataset (Borg et al. 2015b). For the wolf presence model, Recruit was a factor that described the packs' denning success as either "yes" based on the presence of pups in fall, or "no" based on early detection of pups that were not seen with the pack in the fall or repeated pack locations around a suspected or known den site with no visual observations of pups during the summer or fall.

4.2.4 Wolf Sighting Model

We used counts of wolf sightings within sections of the Denali Park Road each year from 1997-2013 as the response variable for a spatially-explicit model to evaluate factors affecting the probability of wolf sightings. We developed eight covariates to represent key processes that we hypothesized would influence wolf sightings and classified these covariates into three categories representing physical (PHYS), biological (BIO), and harvest (HARV) characteristics (Table 4.3). We modeled four different road section lengths (1.6, 3.2, 8.0, and 16.1 km) to investigate the importance of spatial grain size on the probability of sighting. Our section lengths were created to reflect the level of accuracy (1.6 km) of the early (1997-2006) wolf sighting data and 2, 5, and 10-fold increases in section length. The covariates were calculated for each road section length.

The two physical (PHYS) covariates, Vis and Mask, represented an index of the amount of visible area along each road section (Vis) and the likelihood that vegetation would mask the visibility of wolf-sized animals (Mask). We analyzed physical covariates within a 500-m strip on either side of the road because this was the maximum distance wolves were observed from the road. We used the Viewshed Analysis tool in ArcGIS 9.0 to create a raster with 60 by 60 m resolution where each raster cell value represented a measure of how visible a cell was from the Denali Park Road (see Supporting Information for more details). We averaged the values of the visibility raster within each section of road to create the visibility index (Vis). High values of Vis indicate a section of road with highly visible terrain such as wide river bars and open expanses, and low values indicate less visible terrain such as areas where the road corridor was in a valley bottom.

We developed a measure of masking vegetation (Mask) along the road that could hide the presence of a wolf (Fig. 4.3). Vegetation higher than one meter (the average height of a wolf is approximately 0.8 meters) was given a value of 1, and vegetation below one meter was given a value of 0. We averaged the values of the masking raster within each buffered section of road to create the masking index (Mask).

Biological covariates (BIO) included den distance (DenDist), pack size (PackSize), and denning status (DenStatus). PackSize was the size of packs recorded during annual surveys in March for packs with the closest den site. DenDist was the distance of the nearest active den to the closest point on the road for each segment of road in year *t*. We log-transformed DenDist values. Denning status was classified as "successful" based on the presence of pups in fall (recruitment) or "failed" based on early detection of pups that were not seen with the pack in the fall or repeated pack locations around a suspected den site with no visual observations of pups during the summer or fall. We included another classification for cases of packs that denned, as indicated by pups present in the fall, but with uncertain den locations. In these cases "unknown" indicated that the suspected location of the den site or alternate activity center was used to estimate the pack den site location. We included known or estimated den sites for packs with denning information only. Although the number of pups is another potential factor that influenced wolf movements, we lacked reliable pup counts for each pack.

Harvest covariates (HARV) included 3 metrics describing harvest levels of wolves adjacent to DNPP in the season prior to the observation year (*t*). Buffer was the presence or absence of a wolf hunting and trapping buffer located outside of DNPP in the northeast (Fig.4.1) and was a yearly covariate (absent: 1997-1999, 2011-2013, present: 2000-2010). WolfHarv was the number of wolves harvested adjacent to the study region in the regulatory year prior to the sighting year (July year *t*-1 to June year *t*) and was also a yearly covariate. We included all recorded wolf harvest within UCUs 605 and 607 in analyses because these UCUs were within the buffer zone or immediately adjacent to DNPP (Fig. 4.1). UCU 502 extended north beyond DNPP and we therefore attempted to include only instances of wolves harvested within the former buffer zone within UCU 502 using information on the location of harvest. Cases of unknown harvest location within UCU 502 were included in the count of harvested wolves in the region. BHarv was a factor describing if a breeder died in the season prior (yes or no) from the pack near the road segment and was the only spatially explicit harvest covariate.

We developed a candidate model set to represent combinations of the 3 classes of covariates hypothesized a-priori to influence sightings. In addition to these covariates, we included an offset term for the number of trips that passed through each section collecting data to account for variation in observation effort in every model. We also included method of data collection (Collection Type) in all models because model selection criteria indicated improved model fit. We developed a global model that included all terms and evaluated additional models that included reasonable and biologically relevant combinations of covariates.

4.2.5 Statistical Analysis

We used an information-theoretic approach to find the most parsimonious set of independent variables to estimate wolf presence near the road and the probability of wolf sightings. We used the glm function in Program R (R Core Team 2014) to create logistic regression models for wolf presence near the road as a function of covariates described above (n = 14 models). Although interactions between the covariates may influence wolf presence near the road, we did not include interaction or higher level terms in our model set due to limited sample size. For the wolf sighting model, a large number of “zero” counts of wolf sightings per 1.6-km road section (73%, or 702 of 967 counts) resulted in overdispersed count data (mean=0.61, SE=1.84). We modeled the overdispersed count data with a negative binomial regression model, using the glm.nb function in the “pscl” library in program R (Zeileis et al. 2008) to develop count based regression models of wolf sightings as a function of covariates described above (n=29 models). We evaluated multicollinearity among covariates using a variance inflation factor statistic (VIF). All covariates included in the models had a VIF<10 (Kutner et al. 2004).

We used Akaike information criterion (AICc for wolf presence models and AIC for wolf sighting models) to rank models (Burnham & Anderson 2002). To account for model uncertainty, we used model averaging to calculate unconditional parameter estimates and variances. We used the MuMIn package in R (Barton 2014) for model selection and to calculate model averaged parameter estimates and unconditional standard errors. Parameter estimates were considered significant if 95% confidence intervals did not overlap zero. For ease of interpretation of parameter estimates, we back-transformed parameter estimates (β) such that the transformed parameter estimates were equal to e^{β}. The back-transformed parameter estimates are interpreted as odds ratios for the wolf presence model and incidence rate ratios for the wolf sighting model. We calculated the amount of deviance explained by each model (Hagle & Mitchell 1992) as:

$$PseudoR^2 = \frac{model\ deviance - null\ deviance}{null\ deviance}$$

4.4 Results

4.4.1 Wolf Presence Model

Our dataset consisted of locations from 18 wolves that were collared for one to four summers from 2004 to 2012 and had a fix acquisition rate of 80% or higher. Although there was some variability in the proportion of fixes near the road with variable fix acquisition rates (Fig. 4.2), the proportion of fixes near the road was not significantly different when calculated using 1 or 8 fixes per day (t_8 = 2.31, P = 0.41) and samples with 2, 4 or 6 fixes were also not statistically different. We therefore included data from collars with variable fix acquisition rates (1, 2, 6 and 8 fixes per day) in the sample. Five samples (wolf-years) were censored due to lack of den site information. In four of the five censored cases there were zero locations near the road, and in one case the proportion of locations near the road was 0.03. Of the 18 wolves, 12 wolves were breeders and 6 were non-breeders. Our total sample size was 28 wolf-years composed of 21 breeder wolf-years and 7 non-breeder wolf-years. The proportion of locations near the road in our sample ranged from 0 to 0.52 (mean 0.09 ± 0.15 SE)

According to AICc model selection criteria, DenDist, PackSize, WolfStatus, and Recruit were all included in the top ranked models and explained 79% of variation in the proportion of wolf locations that occurred near the Denali Park Road (Table 4.1). The proportion of locations near the road decreased with increasing distance of the den site from the road (β= -0.81 ± 0.048 SE, Table 4.2). Breeding wolves and wolves from larger packs were more likely to be near the road than non-breeding wolves (Status: Non-breeder: β= -1.36 ± 0.189 SE, Pack Size: β= 0.08 ± 0.014 SE). Successful denning increased the probability of wolf presence near the road (β= 0.17 ±

0.150 SE). Parameter estimates for DenDist, PackSize, and WolfStatus were significant, but the confidence interval for the Recruit overlapped zero (Table 4.2).

4.4.2 Wolf Sighting Model

We recorded a total of 589 wolf sightings along the Denali Park Road from 1997-2013. Pack size ranged from 2 – 16 wolves (7.8 ± 4.29 SE), and probability of sightings within road sections (number of sightings divided by the number of trips through the section) and den distances varied with the spatial grain of analyses. The probability of seeing a wolf on a bus trip in a section of road ranged from a mean of 0.005 for 1.6 km road sections to a mean of 0.05 for 16.2 km sections. In addition, the probability of sightings ranged widely among road sections and years within the same spatial grain. For example, sighting probabilities ranged from 0 – 0.22 among the 1.6 km sections and from 0 – 0.39 for 16.2 km sections. Den distances ranged from a mean of 10.6 km for 1.6 km road sections to 6.2 km for 16.2 km sections. During the study period, there were 20 cases of wolves or wolf packs monitored in the study region that were censored because they apparently did not den or we had no denning information available. The number of wolves harvested from the region each year ranged from 0 – 11 (for details, see Borg et al. 2015a).

At all scales (1.6, 3.2, 8.0 and 16.2 km), two models that included Mask, PackSize, DenDist and Buffer received w_i >0.05 and were considered top models (Table 4.3). As anticipated, sightings were negatively associated with the amount of masking vegetation within a given road section (range of incidence ratios for Mask: -0.80 – -0.90, Fig. 4.2, Table 4.5) and positively associated with the amount of visible terrain (Vis: 0.99 – 1.05), although model averaged parameter estimates for the visibility index overlapped zero at all scales (Table 4.5). The incidence of wolf sightings decreased by 0.56 – 0.66% for a 1% increase in den site distance and sightings increased 1.06 – 1.08% for an increase in pack size of one wolf (Fig 4.2). Confidence intervals for parameter estimates for DenDist and PackSize did not overlap zero at any scales of the model (Table 4.5). Successful recruitment at the closest den location increased the incidence of wolf sightings 2.05 – 2.86% compared to denning failure (Table 4.5). Denning success as indicated by estimated den sites likewise suggested an increase in rates of wolf sightings compared to denning failure, but considerable uncertainty surrounded these estimates and their confidence intervals overlapped zero (Table 4.5).

Covariates describing harvest were included in the top models at all scales (Table 4.4). The presence of the trapping and hunting buffer was associated with increased sightings in road segments at every scale (Buffer: present 1.45 – 2.08, Fig. 4.2) and was significant at every scale except 16.2 km sections. The harvest of a breeder was negatively associated with sightings at all scales (BHarv: -0.20 – 0.32), and the number of wolves harvested was negatively associated with sightings at all but the 16.2 km sections (WHarv: 0.004 to - 0.03, Fig. 4.2), although the confidence intervals for the parameter estimates overlapped zero.

4.5 Discussion

Our results highlight the importance of den site proximity to the road corridor, successful recruitment, and pack size to both the probability of a wolf being near the road and the probability of park visitors seeing a wolf. Our analysis further supports a previous finding indicating that harvest of wolves near park boundaries decreased sightings in both Denali and

Yellowstone National Parks when measured on an annual basis (Borg et al., unpublished). Even after accounting for fine-scale variation in sightings due to the physical landscape and the characteristics of packs denning near the road, the negative effect of harvest on sightings remained.

Denning adult wolves are central place foragers, and activity patterns during the pup rearing season are centered around homesites as wolves leave to pursue prey and return at intervals (as reviewed in Mech & Boitani 2003). Previous analyses found that a metric combining den distance and pack size was important in describing variation in the annual probability of wolf sightings along the Denali Park Road (Borg et al., unpublished). Our spatially explicit model partitioned variation in sightings due to den site location and pack size along the road to provide a quantitative measure of the relative impact of these factors. Our analysis shows that den sites are useful and quantifiable predictors of both the proximity of wolves to the road and wolf sightings. An increase in the distance of a den site from the road by 1% decreases the probability of a wolf being near the road by a factor of 0.45 and decreases the incident rate of wolf sightings along a section of road 0.56 – 0.66% (Table 4.2, Table 4.5). Using an estimate of den site location or alternate activity center (DenStatus: unknown, Table 4.5) reflected greater uncertainty in explaining variation in wolf sightings compared to using known den site locations. Pack size likewise influenced wolf proximity to the road and wolf sightings; for an increase of one member to a pack, the probability of a pack members' proximity to the road should increase 1.08 times and the incidence rate for wolf sightings within a road section should increase by 1%. Although the impact of these changes may seem small, wolf sightings are a relatively rare occurrence and the cumulative effects of den site distance and pack size may result in noticeable changes in wolf sightings.

We found that sightings increased during the presence of a trapping and harvest buffer zone compared to the period when there was no buffer zone present. This finding was consistent across multiple scales (Table 4.5) and with the previous analysis of the annual probability of sighting (Borg et al., unpublished). Within each segment of road, the presence of the buffer zone increased the incidence of wolf sightings by 1.45 to 2.08%. Compared to other variables, the magnitude of effect of the buffer zone is notable and would be comparable to increasing the size of the nearest pack by two wolves (Table 4.5). The effect of the buffer zone depends on den site proximity to the road and would have a larger influence when den sites are farther from the road (Fig 4.2). Although managers have little control over the locations wolves choose for denning, maintaining harvest buffers adjacent to parks is a feasible action that might increase sightings, either through positive impacts on wolf pack and population sizes or other, unknown mechanisms.

Although the harvest buffer was associated with increased wolf sightings, the number of wolves harvested from the surrounding region did not clearly explain additional variability in wolf sightings by road segment. The odds ratio ranged from -0.97% – 1% across spatial grains, and there was sufficient uncertainty associated with this parameter that the confidence intervals overlapped zero (Table 4.5). Current harvest records are not sufficient to determine the pack affiliation for wolves harvested in areas adjacent to DNPP (see Methods), and the number of wolves harvested was therefore a yearly covariate and did not incorporate variation due to wolves harvested from specific packs along the Denali Park Road. We recommend increased efforts to track the pack affiliation of wolves harvested adjacent to park boundaries to improve our understanding of how harvest of these wolves may influence wolf sightings.

We found that the breeding status of wolves may influence their role in sightings along the Denali Park Road. Contrary to our predictions, breeding wolves were more likely to be near the road than their non-breeding counterparts. The model averaged odds ratios indicated that the probability of a wolves' presence near the road was 0.26 times lower for non-breeding wolves compared to breeding wolves. We expected that breeder attendance at den sites would decrease their proximity to the road compared to non-breeding wolves. However, rates of den site attendance can be highly variable for breeders (Thurston 2002; Potvin et al. 2004) and thus breeding status may not indicate increased attendance at a den site. In addition, although breeding wolves are typically older and have more experience (Haber 1977; Mech 1999), these factors did not appear to increase wariness or avoidance of the Denali Park Road. Wolves selectively use human made linear travel corridors (James & Stuart-Smith 2000) when traffic and human activity is low (Thurber et al. 1994; Whittington et al. 2005). Through repeated exposure to non-lethal human activity such as vehicle and human traffic along the Denali Park Road, wolves may become habituated to human activity (Schultz & Bailey 1978; Whittaker & Knight 1998) and thus more likely to be near the Denali Park Road. Therefore, breeding wolves may thus contribute disproportionately to visitor sightings of wolves along the Denali Park Road, as they may be more habituated to traffic levels along the road.

In addition, we found that the harvest of a breeder may decrease the incidence of wolf sightings along the Denali Park Road by 0.72 – 0.82%, but the uncertainty in these estimates is high (Table 4.5) and therefore these estimates are not considered significant. Our ability to document harvest of breeders from packs was limited to the sample of collared breeders and was most likely an underrepresentation. In addition to tracking pack affiliation, we recommend recording breeding status of wolves harvested adjacent to park boundaries in the future.

We found that failure to recruit pups was negatively associated with both wolf proximity to the road and probability of wolf sightings. Successful recruitment increased the odds of wolf proximity to the road 1.18 times over instances of where packs failed to recruit pups (Table 4.2). Similarly, successful recruitment increased the incidence of wolf sightings 2.05 to 2.86% over cases where recruitment failed (Table 4.2). The role of successful denning in increasing wolf proximity to the road and sightings indicates another method by which harvest of breeding wolves may disproportionately influence wolf sightings, because breeder mortality can decrease the probability of recruitment (Brainerd et al. 2008; Stahler et al. 2013; Borg et al. 2015)

Although prey abundance and distribution likely influence wolf distribution and therefore sighting probability, the abundance of ungulate prey in the DNPP study area was relatively stable during the years of this study (Adams & Roffler 2009; Owen & Meier 2009; Schmidt & Rattenbury 2013). We assumed that local prey distribution shifts were reflected in our delineation of road sections because our road sections captured broad-scale patterns of local variation in habitat. Additionally, although levels of human activity are known to impact wolves' use of habitat (Whittington et al. 2005; Hebblewhite & Merrill 2008; Musiani et al.

2010), traffic levels along the Denali Park Road were regulated during the study period and subject to the same annual limit and daily traffic levels (NPS 1986).

Our spatially explicit model accounted for variation in sighting probability due to physical parameters along the DPR corridor. The issue of imperfect detection of species has received increased attention (Kellner & Swihart 2014), and terrain and masking vegetation commonly influence detection rates. Our analysis indicates that similar factors relating to physical landscape were important for wolf sightings across several scales. Both physical landscape factors (the amount of masking vegetation and the visibility of the surrounding landscape) were included in the top ranked models, but only the masking covariate was considered significant (Table 4.5). Thus, the effect of masking vegetation along the road had a stronger effect on wolf sightings than the measure of visible terrain. Clearly the type of habitat and vegetation in surrounding areas are important to wolf viewing opportunities (Fig. 4.3), but our analyses provide quantitative measures of the impacts that vegetation can have on wolf sightings. With the amount of shrubs expected to increase with climate change, especially in the Arctic (Walker et al. 2006), vegetative change may reduce opportunities to view wildlife in DNPP and other areas. Land managers specifically tasked with managing for wildlife viewing opportunities should consider the impacts of vegetation change and habitat management, including fire control and suppression and roadside brushing, to the viewing opportunities of the species they manage.

Our spatially explicit model of wolf sightings along the Denali Park Road provides a framework for modeling visitor sightings of terrestrial wildlife. This study is the first to explore the factors that influence park visitor sighting probabilities at multiple spatial scales using detailed covariates describing the surrounding terrain and dynamics of the species of interest. Our physical covariates could apply across broad taxa, and the species-specific covariates could be developed and incorporated into a model to improve our understanding of factors that influence the sightings of other key species.

4.6 Acknowledgements

Funding was provided by the National Park Service and the U. S. Geological Survey. L. D. Mech, L. Adams, J. Burch, B. Dale and T. Meier pioneered the long term study wolf study in Denali National Park and Preserve and collected data from 1986 to 2012. S. Brainerd, G. Hilderbrand, M. Lindberg provided valuable comments on earlier versions of this manuscript. Capture and handling protocols were approved by the National Park Service Institutional Animal Care and Use Committee and are in accordance with recommendations from the American Society of Mammalogists (Sikes et al. 2011). Work was conducted under annual National Park Service permits, annual State of Alaska Department of Fish and Game scientific permits, and the University of Alaska permit (253217-3). Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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4.8 Figures

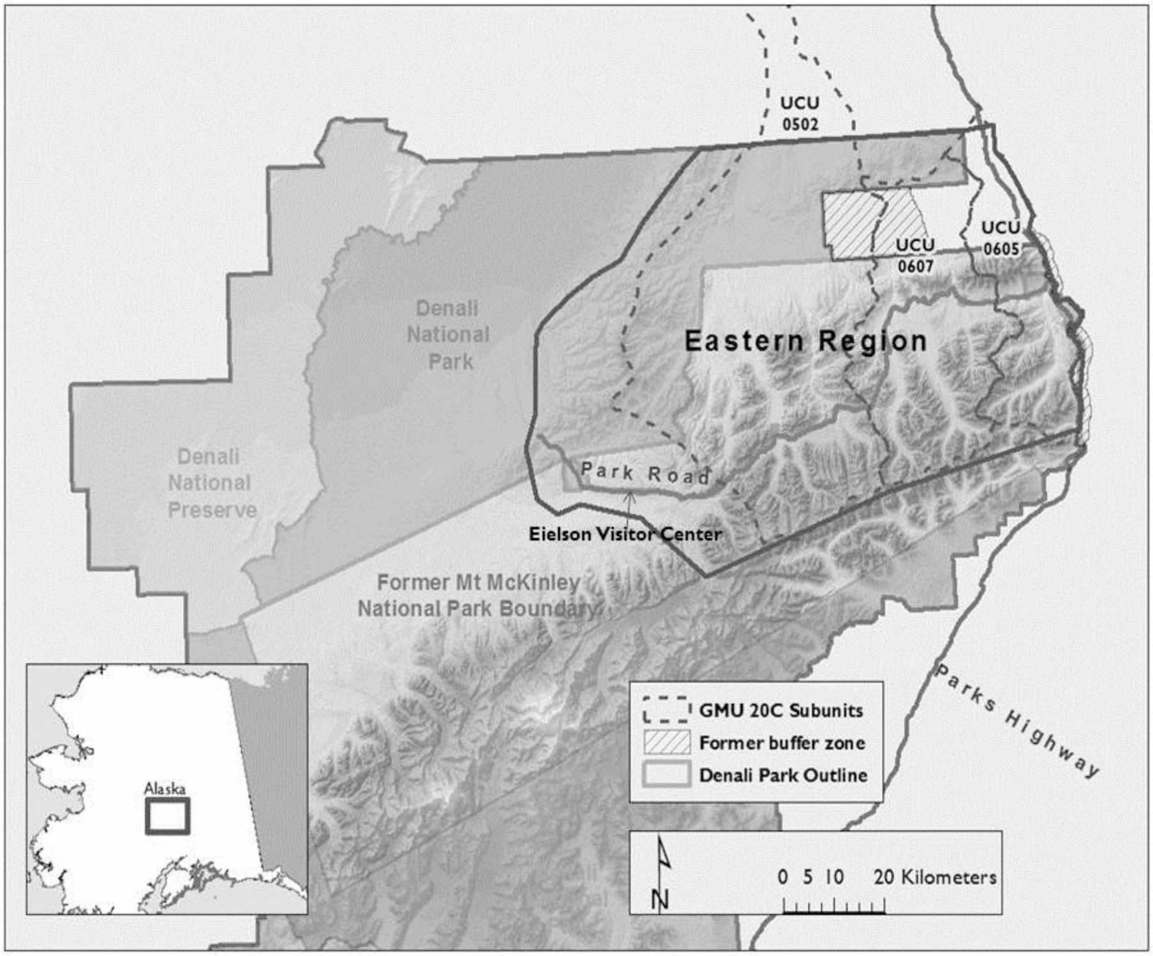


Figure 4.1. Map of study area and geographical sub population regions for long term monitoring of grey wolf packs in Denali National Park and Preserve, Alaska, USA. Uniform Coding Units (UCUs) within Game Management Unit 20C and the former buffer zone where wolf hunting and trapping was prohibited from 2000 to 2010 are shown.

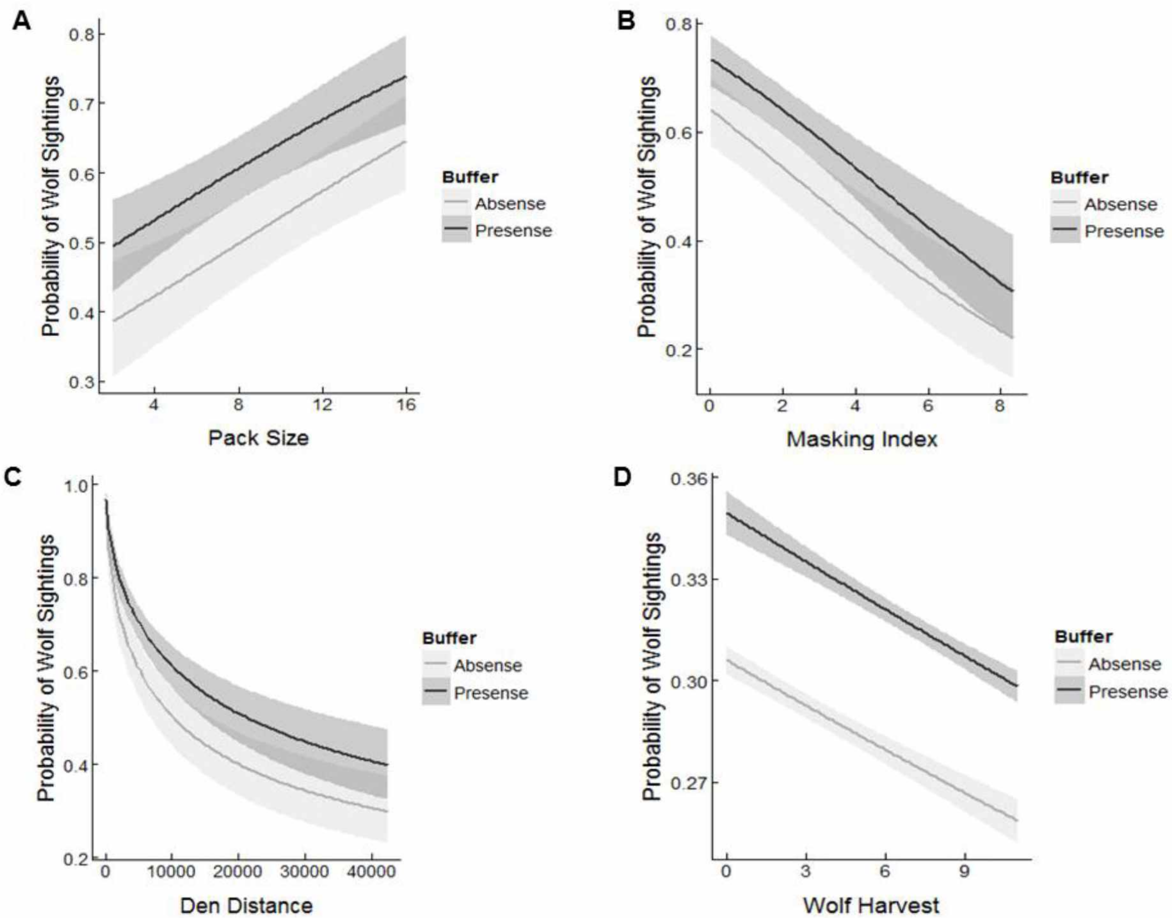


Figure 4.2. Effect of (A) pack size, (B) masking vegetation, (C) distance to the nearest den and (D) number of wolves harvested in the prior year on the probability of wolf sightings along the Denali Park Road in Denali National Park, Alaska, USA, 1997-2013. Shaded areas show 95% confidence intervals around predicted probabilities.

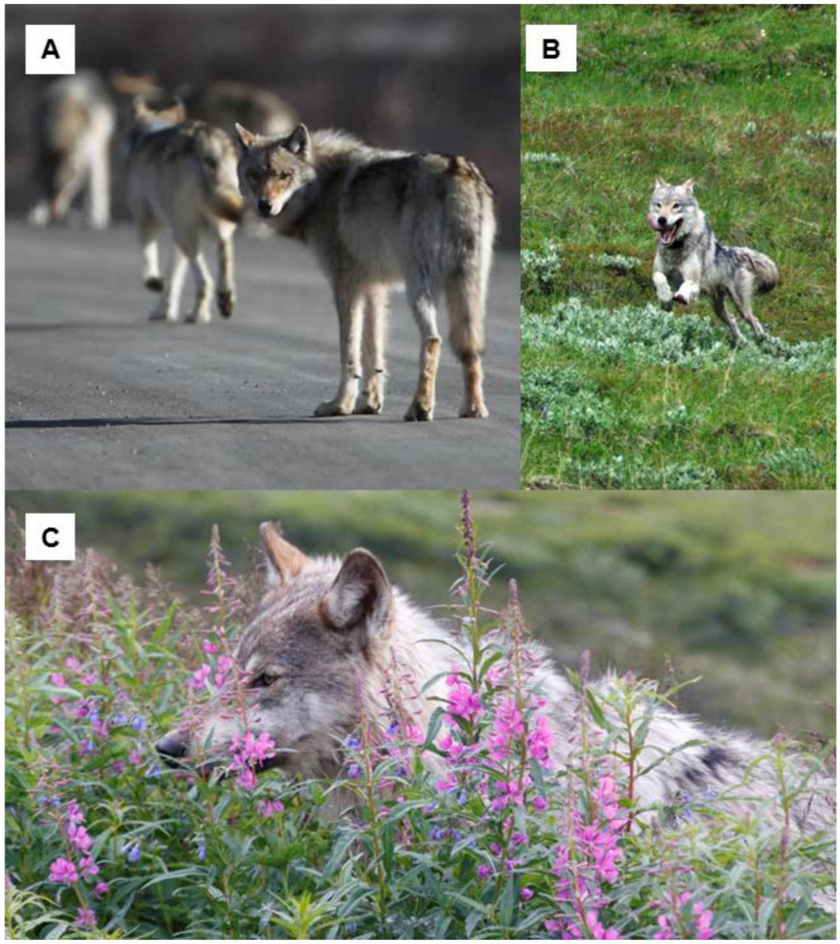


Figure 4.3. Wolves traveling (A) along the Denali Park Road and (B) in short vegetation are easy to see, but (C) a wolf in the surrounding vegetation could be easily obscured, Denali National Park and Preserve, Alaska, USA. NPS Photos.

4.9 Tables

Table 4.1. Candidate model set and model selection criteria evaluating factors affecting the proportion of summer wolf locations near the Denali Park Road in Denali National Park and Preserve, Alaska, USA. K is the number of parameters in the model, DenDist is the log of the distance of the pack den site to the road, PackSize is the size of the pack, WolfStatus is the breeding status of the wolf (Breeder or Non-breeder), Recruit is a factor for success (yes) or failure (no) of denning.

Model	K	AICc	ΔAICc	Model Likelihood	AICc Weight	Log Likelihood	Pseudo-R^2
DenDist+PackSize+WolfStatus	4	294.16	0.00	1.00	0.69	-142.21	0.79
DenDist+PackSize+WolfStatus+Recruit	5	295.73	1.56	0.46	0.31	-141.50	0.79
DenDist+WolfStatus	3	332.98	38.81	0.00	0.00	-162.99	0.75
DenDist+WolfStatus+Recruit	4	335.72	41.55	0.00	0.00	-162.99	0.75
DenDist+PackSize	3	361.28	67.12	0.00	0.00	-177.14	0.72
DenDist+PackSize+Recruit	4	363.80	69.63	0.00	0.00	-177.03	0.72
DenDist+DenStat	3	474.00	179.84	0.00	0.00	-233.50	0.60
DenDist	2	474.27	180.11	0.00	0.00	-234.90	0.60
PackSize+WolfStatus	3	721.49	427.33	0.00	0.00	-357.25	0.34
WolfStatus+Recruit	3	733.29	439.12	0.00	0.00	-363.14	0.33
WolfStatus	2	742.64	448.47	0.00	0.00	-369.08	0.31
PackSize+Recruit	3	1024.20	730.03	0.00	0.00	-508.60	0.02
Recruit	2	1027.87	733.71	0.00	0.00	-511.70	0.01
PackSize	2	1028.85	734.69	0.00	0.00	-512.19	0.01

Table 4.2. Model averaged parameter estimates for model evaluating factors potentially affecting probability of wolf presence near the Denali Park Road in Denali National Park and Preserve, Alaska, USA. DenDist is the log of the distance of the pack den site to the road, PackSize is the size of the pack, WolfStatus is the breeding status of the wolf (Breeder or Non-breeder), DenStatus is a factor for success or failure of denning. β and odds ratio estimates for Status:Non-breeder are relative to Breeders. β and odds ratio estimates for Recruit:Yes are relative to denning failure.

Parameter	β (Model Averaged)	SE	95% CL Lower	95% CL Upper	Odds ratio (Model Averaged)
(Intercept)	2.63	0.281	2.08	3.18	13.89
log(DenDist)	-0.81	0.048	-0.90	-0.71	0.45
PackSize	0.08	0.014	0.05	0.11	1.08
Status: Non-breeder	-1.36	0.189	-1.73	-0.99	0.26
Recruit: Yes	0.17	0.150	-0.13	0.46	1.18

Table 4.3. List and brief description of covariates used in the spatially explicit model of wolf sightings along the Denali Park Road in Denali National Park and Preserve, Alaska, USA from 1997 to 2013.

Covariates	**Description**
Physical (PHYS)	
Vis	Measure of visibility of surrounding terrain from road
Mask	Measure of vegetation tall enough to mask a wolf in the surrounding terrain
Biological (BIO)	
DenDist	Den distance of nearest pack
PackSize	Pack size of nearest pack
DenStat	Den status (denning: success, failed, or unknown)
Harvest (HARV)	
WHarv	Number of wolves harvested in season prior
BHarv	Harvest of a breeder from the near pack in the season prior (yes or no)
Buffer	Presence or absence of hunting and trapping buffer zone
Included in all models	
OFF	Number of trips collecting data that passed through each section
CT	Collection Type (bus driver, NPS staff)

Table 4.4. Candidate model set and model selection criteria evaluating covariates affecting the spatially explicit probability of wolf sightings along the Denali Park Road in Denali National Park and Preserve, Alaska, USA from 1997 to 2013. Collection Type and Offset were included in all models and are not explicitly listed in the covariate set below.

Scale and Models	Log Likelihood	AIC	Δ Log Likelihood	ΔAIC	df	AIC Weight	Pseudo-R^2
1.6 km segments							
17 Mask[14]+PackSize[15]+DenDist[16]+Buffer[17]	-857.40	1726.90	71.00	0.00	6	0.60	0.22
14 Vis[18]+Mask+PackSize+DenDist+DenStatus[19]+Buffer	-855.10	1728.20	73.30	1.30	9	0.31	0.23
3.2 km segments							
14 Vis+Mask+PackSize+DenDist+DenStatus+Buffer	-617.00	1256.00	64.40	0.00	11	0.55	0.28
17 Mask+PackSize+DenDist+Buffer	-620.60	1257.20	60.80	1.20	8	0.30	0.26
1 Vis+Mask+PackSize+DenDist+DenStatus+Wharv[20]+Buffer+Bharv[21]	-616.40	1258.80	65.00	2.80	13	0.14	0.28
8.0 km segments							
17 Mask+PackSize+DenDist+Buffer	-371.70	759.40	34.10	0.00	8	0.53	0.32
14 Vis+Mask+PackSize+DenDist+DenStatus+Buffer	-369.30	760.60	36.50	1.30	11	0.28	0.31
1 Vis+Mask+PackSize+DenDist+DenStatus+Wharv+Buffer+Bharv	-368.80	763.60	37.00	4.30	13	0.06	0.33
16.2 km segments							
17 Mask+PackSize+DenDist+Buffer	-234.20	484.40	28.00	0.00	8	0.30	0.43
26 Mask+PackSize+DenDist	-235.30	484.60	26.90	0.20	7	0.28	0.42
23 Mask+PackSize+DenDist+BHarv	-234.90	485.90	27.30	1.50	8	0.15	0.42
11 Mask+PackSize+DenDist+Wharv	-235.30	486.50	27.00	2.10	8	0.10	0.42
4 Vis+Mask+PackSize+DenDist+DenStatus	-233.90	487.90	28.30	3.50	10	0.05	0.43
14 Vis+Mask+PackSize+DenDist+DenStatus+Buffer	-233.00	487.90	29.30	3.60	11	0.05	0.44

[14] Mask is a measure of vegetation tall enough to mask a wolf in the surrounding terrain
[15] PackSize is the size of the pack denning at the nearest den
[16] DenDist is the distance to the nearest wolf den
[17] Buffer is a factor indicating the presence or absence of a wolf harvest buffer
[18] Vis is a measure of visibility of surrounding terrain from road
[19] DenStat is a factor indicating if denning was successful
[20] WHarv is the number of wolves harvested the season prior
[21] BHarv is a factor indicating if a breeder was harvested from the nearest pack

Table 4.5. Model averaged parameter estimates for model evaluating covariates affecting the spatially explicit probability of wolf sightings along the Denali Park Road in Denali National Park and Preserve, Alaska, USA from 1997 to 2013. Collection Type and Offset were included in all models and are not explicitly listed in the covariate set below. β and odds ratio estimates for DenStatus are relative to denning failure (failure to recruit pups). β and odds ratio estimates for Buffer are relative to absence of the buffer zone. IR indicates incidence ratios (e^{β}). Confidence intervals for estimates in italics overlap zero. Light grey text indicates that parameters were not included in top models ranked by AIC.

Parameter	**1.6 km sections**		**3.2 km sections**		**8.0 km sections**		**16.2 km sections**	
	β±SE	IR	β±SE	IR	β±SE	IR	β±SE	IR
PHYS								
Vis[22]	*0.02±0.04*	*1.02*	*0.01±0.04*	1.01	*0.05±0.06*	1.05	*-0.01±0.12*	*0.99*
Mask[23]	-0.21±0.03	0.81	-0.22±0.04	0.80	-0.10±0.04	0.90	-0.17±0.05	0.84
BIO								
DenDist[24]	-0.58±0.07	0.56	-0.58±0.08	0.56	-0.41±0.07	0.66	-0.41±0.07	0.66
PackSize[25]	0.07±0.02	1.07	0.06±0.02	1.06	0.07±0.02	1.07	0.08±0.03	1.08
DenStatus[26]: success	1.05±0.35	2.86	0.92±0.38	2.51	0.92±0.45	2.51	*0.72±0.46*	*2.05*
DenStatus: unk	*0.50±0.66*	*1.65*	*0.34±0.65*	1.40	*0.88±0.78*	2.41	*0.90±0.76*	*2.46*
HARV								
WHarv[27]	*-0.03±0.03*	*0.97*	*-0.02±0.03*	0.98	*-0.01±0.05*	0.99	*0.004±0.04*	*1.00*
BHarv[28]	*-0.23±0.40*	*0.79*	*-0.30±0.21*	0.74	*-0.20±0.42*	0.82	*-0.32±0.42*	*0.73*
Buffer[29]: present	0.73±0.18	2.08	0.70±0.19	2.01	0.64±0.22	1.90	*0.37±0.25*	*1.45*

[22] Vis is a measure of visibility of surrounding terrain from road
[23] Mask is a measure of vegetation tall enough to mask a wolf in the surrounding terrain
[24] DenDist is the distance to the nearest wolf den
[25] PackSize is the size of the pack denning at the nearest den
[26] DenStat is a factor indicating if denning was successful
[27] WHarv is the number of wolves harvested the season prior
[28] BHarv is a factor indicating if a breeder was harvested from the nearest pack
[29] Buffer is a factor indicating the presence or absence of a wolf harvest buffer

4.10 Supporting Information

Appendix S4.1. Denali Park Road Viewshed Analysis

Objective

We created a viewshed raster of the features along the Denali Park Road (DPR) which provides a quantitative measure of visibility of the surrounding terrain along the DPR. The DPR viewshed can be analyzed in conjunction with locations of collared animals to determine patterns of visibility in relation to wildlife movements. We developed a tool that outputs a viewshed raster that increases the value of the raster cell by one if the location is visible from an observation point. When iterated over a series of points (or along a line), the result is a raster with a range of values with the highest values occurring at cells that are visible from the most locations. This provides a quantifiable measure of the most visible landscape features.

Methods

Height of vegetative cover can greatly impact visibility along the DPR by blocking line of sight. We created a 5 km buffer along either side of the DPR, clipped the landcover within the buffer and summarized the landcover classes within the buffer to determine predominate landcover classes within 5 km of the road. We created estimates of average height for each class of predominant land cover (Table S4.1). Vegetation is cleared on either side of the road 16’ from the edge of the roadbed. We combined average height of vegetation cover and digital elevation models (DEM) to create a raster of visible landscape for use in visibility analysis. Our analysis assumes no vegetation 7 meters from the center of the DPR, accounting for the roadbed and low vegetation resulting from park brushing operations.

We used the Feature Vertices to Points tool in the ArcGIS 9.0 (Environmental Systems Research Institute, Redlands, CA) to generate a dataset of 5171 points at vertices along the DPR and the Viewshed tool to conduct the visibility analysis (for more details see http://help.arcgis.com/en/arcgisdesktop/9.0/). The extent of the analysis was limited to the DNP boundaries and therefore does not include areas to the east of the park that may be visible when traveling east along the park road.

Results

The maximum cell value (corresponding to the maximum number of locations from which a cell is visible) is 2863 (Table S4.1). The output viewshed raster produced from this analysis is available on the Alaska Regional National Park Service permanent dataset.

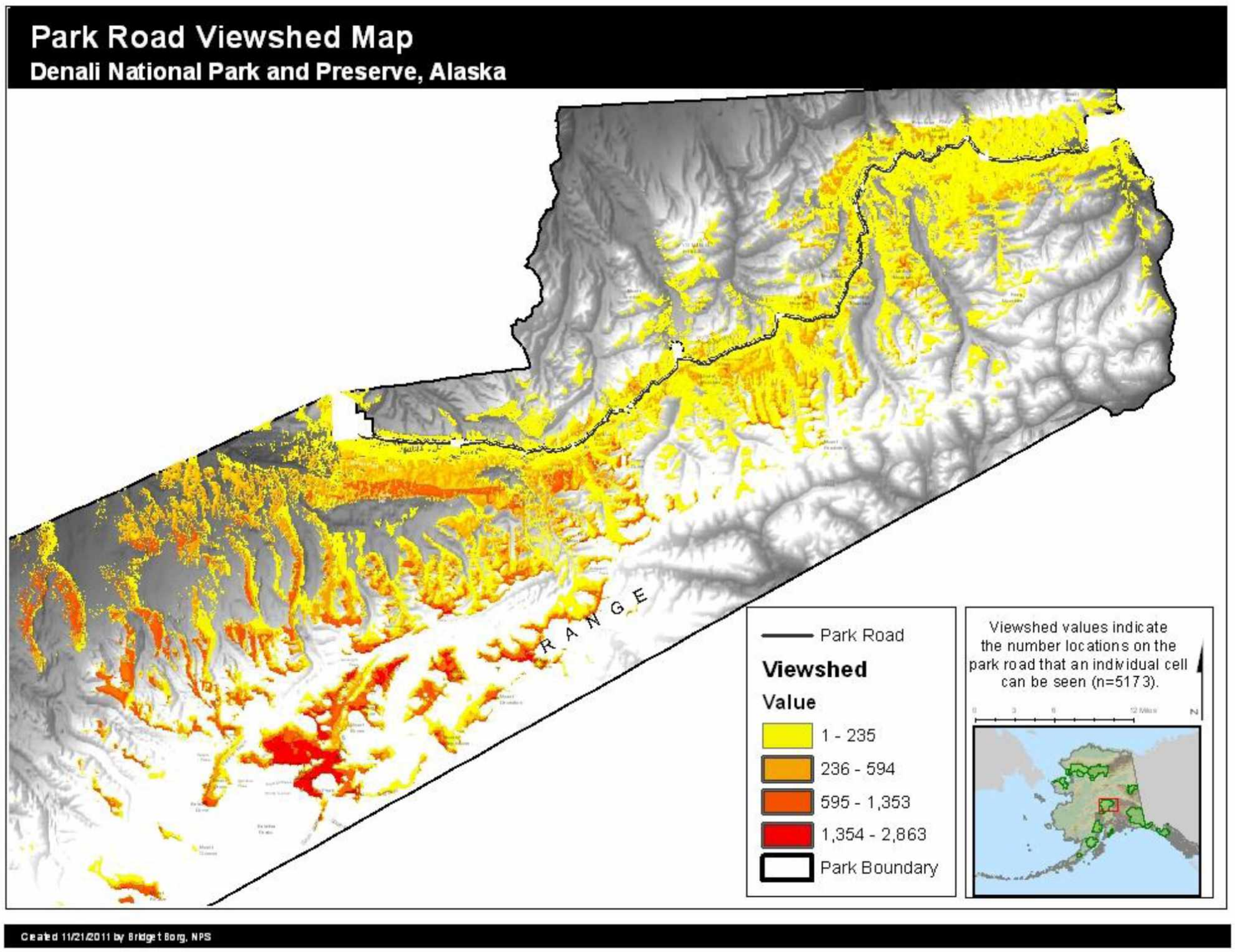
TABLES

Table S4.1. Estimated mean height of landcover classes along the Park Road.

Vegetation Class	Mean height (m)
Alder	3.0
Bare Ground	0.0
Broadleaf	8.0
Clear Water	0.0
Closed Low Shrub Birch	1.5
Cloud	n/a
Dense-Open Spruce	10.0
Dry-Mesic Herbaceous	0.8
Dwarf Shrub	0.2
Dwarf Shrub-Rock	0.2
Low Shrub-Sedge	0.5
Low Shrub Birch-Ericaceous-Willow	0.5
Open-Woodland Spruce	10.0
Shadow-Indeterminate	n/a
Silty Water	0.0
Snow-Ice	0.0
Sparse Vegetation	0.0
Spruce-Broadleaf	10.0
Stunted Spruce	4.0
Wet Herbaceous	0.5
Willow	2.0

FIGURES

Figure S4.1. Map displaying viewshed tool raster output from analysis on a set of 5171 points along the Denali National Park Road, Alaska.



Chapter 5

Conclusions

In the introduction, I discussed how a Structured Decision Making (SDM) process could be applied to the issue of transboundary management of wolves in and adjacent to Denali National Park and Preserve (DNPP). In the initial steps of the process I defined the problem, established potential objectives, defined a limited set of potential actions, and discussed consequences. The "consequences" step requires developing models that link the actions to the outcomes. In the conclusion, results from chapters 2 – 4 are used to develop models of the system and incorporate structural uncertainty. I conclude by discussing the final steps of the SDM process: defining an optimal solution and implementing the action, and consider how two additional steps, monitoring and learning, can be applied in an adaptive management approach.

5.1 Steps to a Structured Decision Making Process

5.1.1 Step 4. Consequences (revisited)

The objective for this step is to develop models that link the management action (i.e. opening or closing the Wolf Townships to harvest) to measurable attributes of our objectives (i.e. consumptive and non-consumptive use of wolves). Findings from chapters 2 – 4 are incorporated into a basic model relating the probability of wolf sightings, P_s to the management action, A, defined as the opening or closing of the Wolf Townships to harvest. I discuss how information on wolf harvest adjacent to DNPP, specifically the number of wolves harvested, $W_{h,}$, and harvest opportunities, $W_{o,}$ could be used to develop a model relating these attributes to the management action, *A*. These two models of the system are incorporated into a utility function, quantifying the benefit of the action under various scenarios.

5.1.1.2 Model 1: Wolf sighting response to management action

In chapter 2, we found that harvest of breeders increased the probability of pack dissolution, likely because the timing of harvest coincided with the breeding season of wolves. We also found packs that lost breeders exhibited lower denning and recruitment rates than those that did not experience breeder loss. In chapter 4, we found that denning success increased wolf sightings. Therefore, decreased denning and recruitment rates maybe a mechanism by which harvest of breeders may decrease wolf sightings.

In chapter 3 we found that both the number of wolves denning near the road and wolf harvest influenced the mean probability of viewing wolves in DNPP. A metric that combined the number of wolves and the proximity of the den site to the road (PackNearRoadIndex or PNRI) was positively associated with the probability of viewing wolves (PNRI: $\beta = 24.6 \pm 3.13$ SE). The presence of the buffer was also positively associated with the probability of viewing wolves (Buffer presence: $\beta = 1.0 \pm 0.17$), whereas the number of wolves harvested in the prior year was negatively associated with the probability of viewing a wolf (WolfHarv: $\beta = -0.1 \pm 0.02$). In chapter 4 we found that compared to other variables, the magnitude of effect of the buffer zone was notable and would be comparable to increasing the size of the nearest pack by two wolves, or the proximity of the nearest den site to the road approximately 4 km. In short, accounting for wolf pack size, den distance, and denning success, the effects of the management action on the probability of wolf sightings remained, with the closure of wolf harvest in the "buffer zone" predicted to result in a measurable increase in wolf sightings.

If spatially explicit factors such as the amount of masking vegetation were predicted to change during the time frame for the decision, or a more refined approach to addressing den distance, denning success, and pack size were desired, then a spatially explicit model (Chapter 4) would be recommended. Otherwise, for the relative simplicity of developing the model, P_s can represent the annual probability of sighting, expressed as a function of the distance of den sites from the road (DenDist), pack size (PackSize), den success (Recruit), number of wolves harvested (W_h), number of breeding wolves harvested (B_h), and the action of opening or closing the Wolf Townships to harvest (A):

$$P_s = F[DenDist, PackSize, Recruit, W_h, B_h, A] \qquad (1)$$

estimates from chapter 3 and 4 (Table 3.2, Table 4.5) could be used as a starting points for the estimates for the effect size of DenDist, PackSize, Recruit, W_h, B_h, and A.

Several models could be developed to address structural uncertainty remaining in the model of the system (Williams et al. 2002; Martin et al. 2011). Structural uncertainty can be expressed in a discrete set of alternative models in which the model structure or parameter estimates for the effect of interest are varied under alternate hypotheses. For example, uncertainty in the effect of the number of wolves harvested, W_h, on wolf sightings, P_s, could be addressed be developing one model in which the effect of W_h would be strong and an alternate model, where the effect of W_h

would be weak. For the initial assessment, the models could be assigned equal weights or weights reflecting relative support based on expert knowledge of the system. In the adaptive management approach, the model weights would be updated based on the observed response of the system following implementation of the management action.

5.1.1.2 Model 2: Harvest/harvest opportunity response to management action

Determining how the action of closing the Wolf Townships affects opportunities for consumptive use of wolves depends on the measurable attribute for consumptive use. The model linking the objective for consumptive use of wolves to the management action could be expressed either by W_o, representing wolf harvest opportunities, W_h, representing the number of wolves harvested, or a combination of the two.

As discussed in the introduction, harvesting a wolf is challenging, unpredictable, and subject to random chance. Therefore W_h may not reflect the fundamental objective for consumptive use of wolves, if the fundamental objective emphasized providing opportunity for wolf harvest as opposed to the number of wolves harvested. A measure of wolf harvest opportunity, W_o, such as number of active users, number of traplines maintained, etc. may be an appropriate measurable attribute for this objective, although admittedly, this information may be difficult or unrealistic to obtain. Alternatively, stakeholders could create a subjective value for the opening of the Townships in terms of its increase in wolf harvest opportunities, reflecting an increase in the area open for harvest activities, for example:

$$W_o = \begin{cases} 2 \; if \; A = Open \\ 1 \; if \; A = Close \end{cases} \tag{2}$$

Although closure of the Wolf Townships may decrease opportunity for harvest activities, harvest closure in this small area does not necessarily mean the number of wolves harvested in the wider region would be reduced. In Chapter 3, we summarized harvest of wolves in Uniform Coding Units (UCUs) adjacent to the eastern region of DNPP from 1996 to 2012 (Chapter 3, Table S3.1). Based on this summary, during the presence of the buffer zone, harvest of wolves adjacent to DNPP (7 ± 11.25 SE) was on average greater than during the period without the presence of the buffer zone (2.6 ± 4.3, t_{12}=2.18, P=0.02). This pattern reflects the fact that the buffer zone did not encompass the entirety of the UCUs overlapping and adjacent to the DNPP boundaries (Figure 1-1) and wolves were harvested in areas of the UCUs open to harvest during presence of the buffer zone. These findings show it is important to explicitly define the region of interest when creating the fundamental objectives for harvest, because the models describing the system would be fundamentally different if closure is restricted to a small area within the Wolf Townships or encompassed the entire UCUs adjacent to DNPP boundaries.

We lack an accurate estimate of the annual trapping and hunting effort during the presence and absence of the buffer zone to control for changes in effort during these periods. In developing a model of the response of W_h to A, it would be important to consider a variable representing harvest effort. However, the numbers of active trappers in the Wolf Township is low, with between one to three trappers that seal hides within UCU 605, 607 and 503 in any given year (ADF&G 2013a). Thus, it may be reasonable to assume a relatively consistent level of effort or the effort varies randomly in our models.

The wolf population size in DNPP (and presumably in adjacent areas) was also higher during the presence of the buffer zone (Borg & Burch 2014) which may account for increased number of wolves harvested during that period and a measure of wolf population size, WolfPop, should be explicitly considered in the model. Additionally, in order to ensure that the harvest occurs according to sustained yield principles, the objective for the number of wolves harvested should be framed in terms of total yield, current and future (Williams et al. 2002; Conroy & Carroll 2009). The influence of harvest in one year on the population and future harvest opportunities will depend on several variables including current population size, natural growth rate of the population, λ, and relationship of harvest to population dynamics, D_h, (Williams et al. 2002; Fuller et al. 2003; Adams et al. 2008; Smith et al. 2010) and can be expressed as:

$$W_h = F[WolfPop, Effort, D_h, \lambda, A] \quad (3)$$

5.1.1.3 Utility function

The "combined objective" example created in the introduction (Chapter 1) seeks to maintain wolf viewing opportunities above a threshold while allowing or maximizing wolf harvest opportunities. The objective can be formalized mathematically as a utility (or objective) function. The utility function quantifies the benefit obtained by implementing the action (Williams et al. 2002; Martin et al. 2011). The utility function for the combined objective can be expressed as:

$$U_t = \alpha_h * \alpha_s \quad (4)$$

where U_t is the utility function at time *t*, where α_h represents the expected benefit of action *A* for wolf harvest objectives and α_s is a penalty factor. α_h could be formulated as:

$$\alpha_h = W_h * W_o \quad (5)$$

and α_s as:

$$\alpha_s = {}^{1}/_{(1 + exp\{\tau - E[P_s|DenDist, PackSize, Recruit, WHarv, BHarv, A]\}} \quad (6)$$

The expected probability of wolf sightings, given important variables (Eq. 1) is expressed as:

$$E[P_s|DenDist, PackSize, Recruit, W_h, B_h, A] \quad (7)$$

and τ is the utility threshold (i.e. the desired probability of wolf sightings). The utility threshold would be determined by the stakeholders (Martin et al. 2009) and any action that decreases the wolf viewing opportunities below τ, would be greatly devalued. According to equation 6, if the $E[P_s] \ll \tau$, then α_s approaches 0 and if $E[P_s] \gg \tau$, then α_s approaches 1. The idea is to maximize the utility function. The utility function will be highest when both components are maximized. The wolf sighting component is maximized when the expected probability of sightings ($E[P_s]$) is much greater than the threshold, τ. The wolf harvest component is maximized when the Wolf Townships are open to harvest, and the expected number of wolves harvested, current and future, is maximized.

5.1.2 Step 5. Optimal solution

Although one action may dominate in its ability to meet one objective, there may be obvious tradeoffs for meeting multiple objectives, and it is important to explicitly recognize trade-offs before making a decision. Based on findings presented in my thesis, it appears that closure of the buffer zone would present the optimal solution. The presence of the buffer did not decrease wolf harvest or presumably harvest opportunities in the region surrounding the Wolf Townships, and the buffer was associated with substantially increased wolf sightings. It is possible that the higher wolf population size, harvest levels, and sightings during the buffer years were coincidental and not related to the buffer itself but some other unknown factor. Resolving this structural uncertainty would require additional years of monitoring the response of the system with the buffer zone in place.

Nevertheless, consideration of the trade-offs is critical. The closure of the Townships to harvest may represent a decrease in trapping and hunting activities that are themselves important and unrelated to the number of wolves harvested or a quantifiable measure of harvest opportunity. Hunting and trapping are important parts of Alaskan culture and there is a desire to maintain the culture and knowledge related to trapping specifically ("Alaska Trappers Association" 2015). It has been suggested that given the large number of visitors to DNPP and the relatively small number of trappers and hunters active in the Wolf Townships, that the closure of the Townships to wolf harvest is a negative impact for a few with a positive outcome for many (Mowry 2013). Indeed, annually over 400,000 people visit DNPP (Fix et al. 2012), while the numbers of active trappers in the Wolf Township is between 1-3 in any given year (Alaska Department of Fish and

Game 2013a). However, the impact of the closure to the lifestyle and livelihood of these trappers may represent a significant trade-off and should not be discounted.

In addition, the economic values of consumptive and non-consumptive uses of wolves are worth consideration. Wildlife viewing is a driver of tourism for DNPP as well as for the state of Alaska and brings an important socio-economic benefit to the states (Stynes & Ackerman 2010; U. S. Department of the Interior et al. 2011). At the same time, harvest of wolves can provide significant economic benefits as well (National Research Council 1997). The relative magnitude of these economic impacts are currently unknown, but there is a collaborative effort between the NPS and ADFG to quantify the economic benefits of consumptive and non-consumptive uses of wolves in and adjacent to DNPP to provide an estimate of the economic trade-offs (D. Schirokauer, pers. comm).

It is also important at this stage in the SDM process to perform sensitivity analysis to examine how the optimal decision and expected performance is affected by the assumptions, problem framing, parameters in the models, and levels of uncertainty. It would also be important to vary the threshold estimate, τ, and provide a range of values for the system state variables to investigate their influence on the outcome of the utility function, U_t.

5.1.3 Step 6. Implement the action

Once the optimal decision has been identified and the tradeoffs and uncertainty are recognized, a vital step is to take action. In the SDM approach relating to a one-time decision, this would be the last step in the process, although ideally, monitoring of both harvest and wolf sightings would continue to help understand how they responded to management actions. If the decision was to be made on a repeated basis, for example, if the decision to open or close the Townships to wolf harvest was to be made at the beginning of every regulatory year, the following additional steps of monitoring, assessment and learning would be included in an adaptive management framework.

5.1.4 Step 7. Monitor

The purpose of monitoring is to: 1) determine if the objectives are being met, 2) assess the state of the system for the purpose of making decisions dependent on the state of the system, and 3) resolve uncertainty and improve the models that explain our understanding of the system (Nichols & Williams 2006). In order to determine if our objectives are being met, monitoring should be focused on the performance criteria defined in our objectives (i.e., monitoring harvest rate and probability of wolf viewing). Monitoring should also include the identified system state variables as described in the models, most of which occur as part of long term monitoring protocols for DNPP's wolf project (Meier et al. 2009) or through state of Alaska monitoring of harvest. I include several recommendations for improving the current monitoring in order to refine our understanding of the system.

All wolves harvested (shot or trapped) are required by law to be sealed with ADFG (Alaska Department of Fish and Game 2013b). However, the size and shape of the recording units (UCUs) adjacent and overlapping the DNPP boundaries make it difficult to tell where a wolf was harvested (Fig 1.1). Refining the recording units or creating subunits to delineate harvest of wolves within the Wolf Townships would improve our ability to infer how the harvest of wolves in this area influences wolf sighting opportunities. Alternatively, any action considered (opening or closing wolf harvest or implementing quotas or bag limits) should be implemented within the same spatial extent as the recording units (UCU). For example, opening or closing harvest should occur within the entirety of specified UCUs.

Current harvest records are not sufficient to determine the pack affiliation for wolves harvested in areas adjacent to DNPP. Increased efforts to track the pack affiliation of wolves harvested adjacent to park boundaries would improve our understanding of how harvest of these wolves may influence wolf sightings. Monitoring of wolf packs and efforts to maintain collars on wolves in each pack is a goal of long term monitoring program in DNPP. As part of this program, I recommend formally documenting breeding status of wolves, closer monitoring of packs in the eastern region of the park, and increased efforts to track breeding status of wolves harvested adjacent to DNPP boundaries (Chapter 4).

Moveover, I recommend further research into the effect of harvest on population dynamics in the wolf system in and adjacent to DNPP. Although there is research on the effects of harvest on wolf populations in other regions (Fuller et al. 2003; Adams et al. 2008; Smith et al. 2010; Creel & Rotella 2010; Murray et al. 2010; Sparkman et al. 2011), the relationship appears variable and may depend on characteristics of the system and population studied. Information from research in this study system could directly improve the model of the system (Eq. 6).

5.1.5 Step 8. Learning

Adaptive management can reduce the uncertainty related to how system dynamics respond to management actions by learning from the response of the system to management action. In this example, I discussed how models representing alternate hypotheses can incorporate uncertainty related to the effect of harvest on wolf sightings and wolf harvest opportunities. Each model makes a prediction of how the system will respond to the action. To start, each model in a model set is given a weight, either based on a priori knowledge of how the system works or subjectively. After the optimal solution is defined and implemented in the preceding steps, the prediction is compared to the observed result (as seen through monitoring) and model weights are updated using Bayes Theorem.

Bayes Theorem basics

The new weight of the model i is a function of the old weight of the model i and the likelihood of the new data according to the model i.

The updated model weights represent our relative faith in the models given the data we observed. Under the conditions that each model fairly represents the idea that generated it, an adequate monitoring system is in place, and there is a good approximating model within the model set, then over time the process will further learning and one model may become dominant. In the next time step, the updated model weights will be used to generate a prediction of the system under the alternative actions, given the new system state and the process can be repeated iteratively.

Double-loop learning

In addition to learning through time by confronting models with data and updating model weights, the whole adaptive management process can be subject to “double loop learning” (Argyris 1976). This means that over time we should revisit our problem and reevaluate whether our objectives, alternative actions and available model sets can be improved based on what we have learned, how the system has changed, and how management objectives or perspectives may have changed (Argyris & Schon 1978).

This process could be especially pertinent to the issue of wolf harvest regulation in the Wolf Townships. The fundamental objectives of stakeholders are subject to change over time, as well as the framing or nature of the problem itself. Even through the SDM framework for a one-time decision, the process of elucidating the objectives, defining potential actions, creating models and developing optimal solutions can yield valuable insight. SDM and adaptive management provide a valuable and transparent method for decision making in the face of competing objectives and uncertainty. The issue of transboundary wolf movements and associated management conflicts are not unique to DNPP and the Wolf Townships, and this example could provide a valuable framework for implementing a formal decision-making process to address similar issues.

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